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New fossil dermestid beetles (Coleoptera: Dermestidae) from the Baltic amber – III

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Abstract. New representatives of dermestid beetles are described from the Late Eocene to Early Oligocene inclusions of the Baltic amber, i. e. *Anthrenus* (*Nathrenus*) *kerneggeri* sp. nov., *Attagenus balticus* sp. nov., *A. obesus* sp. nov., *Evorinea amberica* sp. nov. and *Phradonoma ambericum* sp. nov.

Taxonomy, new species, description, fossil, Coleoptera, Dermestidae, Tertiary, Eocene, Oligocene, Baltic amber

INTRODUCTION

Family Dermestidae is a diverse group with number of cosmopolitan species comprising about 1300 species in recent fauna (Háva 2003, 2008, Lawrence & Slipinski 2005). Fossil record of dermestid beetles is well known especially from Cenozoic era of Baltic and Dominican ambers, but also from lacustrine deposits of Europe and North America (Carpenter 1992, Wappler 2003). An attribution of the Late Triassic genera from Queensland (Australia) to the family Dermestidae based on elytra structure are considered as family uncertain assignments (see Carpenter 1992).

The present study follows of the preceding papers on fossil dermestid beetles from Dominican and Baltic ambers (Háva & Prokop 2004, 2006, Háva et al. 2006a, b). Baltic amber is the world most well-known source of amber inclusions dated from Late Eocene to Early Oligocene between 35 to 45 Ma (Ross 1998).

MATERIAL AND METHODS

Material of insect inclusions is preserved in polished pieces of transparent amber protected against weathering and damage by embedding in the synthetic resin (GTS / 2-component resin) or at least covered with lacquer. Standard techniques of observation by stereomicroscope (Olympus SZX 9) and digital photography (Olympus 5060) were used. The integumental structures are named according to Harris (1979).

Because the size of the beetles or their body parts can be useful in species recognition, the following measurements were made: total length (TL) – linear distance from anterior margin of head to apex of elytra, elytral width (EW) – maximal linear transverse distance.

Material examined for this study is housed in the following museums and private collections abbreviated by acronyms:

JHAC – Jiří Háva, Private Entomological Laboratory and Collection, Únětice u Prahy, Czech Republic;
FKHC – Friedrich Kernegger, private collection, Hamburg, Germany;
GPIH – Geologisch-Paläontologisches Institut der Universität Hamburg, Germany.

Additional photographs of the all presently described species are available also on the internet web sites: Dermestidae World (Coleoptera), World Wide Web electronic publication (see Háva 2008).

SYSTEMATIC PALAEONTOLOGY

***Anthrenus* (*Nathrenus*) *kerneggeri* sp. nov.**

(Figs 1, 2, 10)

Type material (holotype). Baltic amber inclusion No. 144/2001, Jantarnyj, Kaliningrad District, Russia. Holotype deposited in GPIH. Holotype specimen is provided with a red, printed label with text as follows: "HOLOTYPE, *Anthrenus* (*Nathrenus*), *kerneggeri* sp. nov., J. Háva, J. Prokop & A. Herrmann det. 2005".

Description of holotype. Measurements (mm): TL 1.9 EW 1.3. Body black, oval (Fig. 1). Dorsal surface covered by black and white scales (Fig. 1). Individual scales setiform, very narrow. Antennae black, 11 antennomerae; antennal club 3 antennomerae, black, compact, terminal segment regularly rounded. Eyes, large, with entire median margin and with microsetae. Frontal median ocellus presented. Pronotum covered with white scales and medially with black scales (Fig. 10). Elytra covered by black and white scales; black scales forming three transverse band, combined medially, epipleuron with white scales. Ventral surface covered only with white scales (Fig. 2). Prosternum only with white scales. Metasternum with only white scales, without a large patch of black scales at lateral margins. Abdominal sternites not bearing larger spots of black scales at antero-lateral margins. Sternites I–IV without one large spot of black scales in the middle. Legs dark-brown to black with white setation and white scales. Genitalia not visible.

Discussion. The new *Anthrenus* species belongs to the subgenus *Nathrenus* Casey, 1900. The subgenus *Nathrenus* differs from other subgenera by the following characters: antennae 11 antennomerae, eyes with median margin complete. The new species habitually similar to the three known fossil species (*A. (N.) electron* Háva, Prokop et Kadej, 2006, *A. (N.) groehni* Háva, Prokop et Herrmann, 2006 and *A. (N.) ambericus* Háva, Prokop et Herrmann, 2006). It differs from them by the combination of the characters provided in the following key:

1(6) dorsal surfaces covered by bicolorous scales; each elytron with patches.
2(3) abdominal sternites not bearing small spots of black scales at antero-lateral margins; elytra covered by black and white scales; black scales forming three transverse band, combined medially. .... *A. (N.) kerneggeri* sp. nov.
2(3) abdominal sternites bearing small spots of black scales at antero-lateral margins.
4(5) elytra covered by black and white scales; black scales forming transverse band and apical spot. .... *A. (N.) electron* Háva, Prokop et Kadej, 2006
5(4) elytra covered by black scales with small circular patches of yellow scales. .... *A. (N.) groehni* Háva, Prokop et Herrmann, 2006
6(1) dorsal surfaces covered by unicolorous scales; each elytron without patches. .... *A. (N.) ambericus* Háva, Prokop et Herrmann, 2006

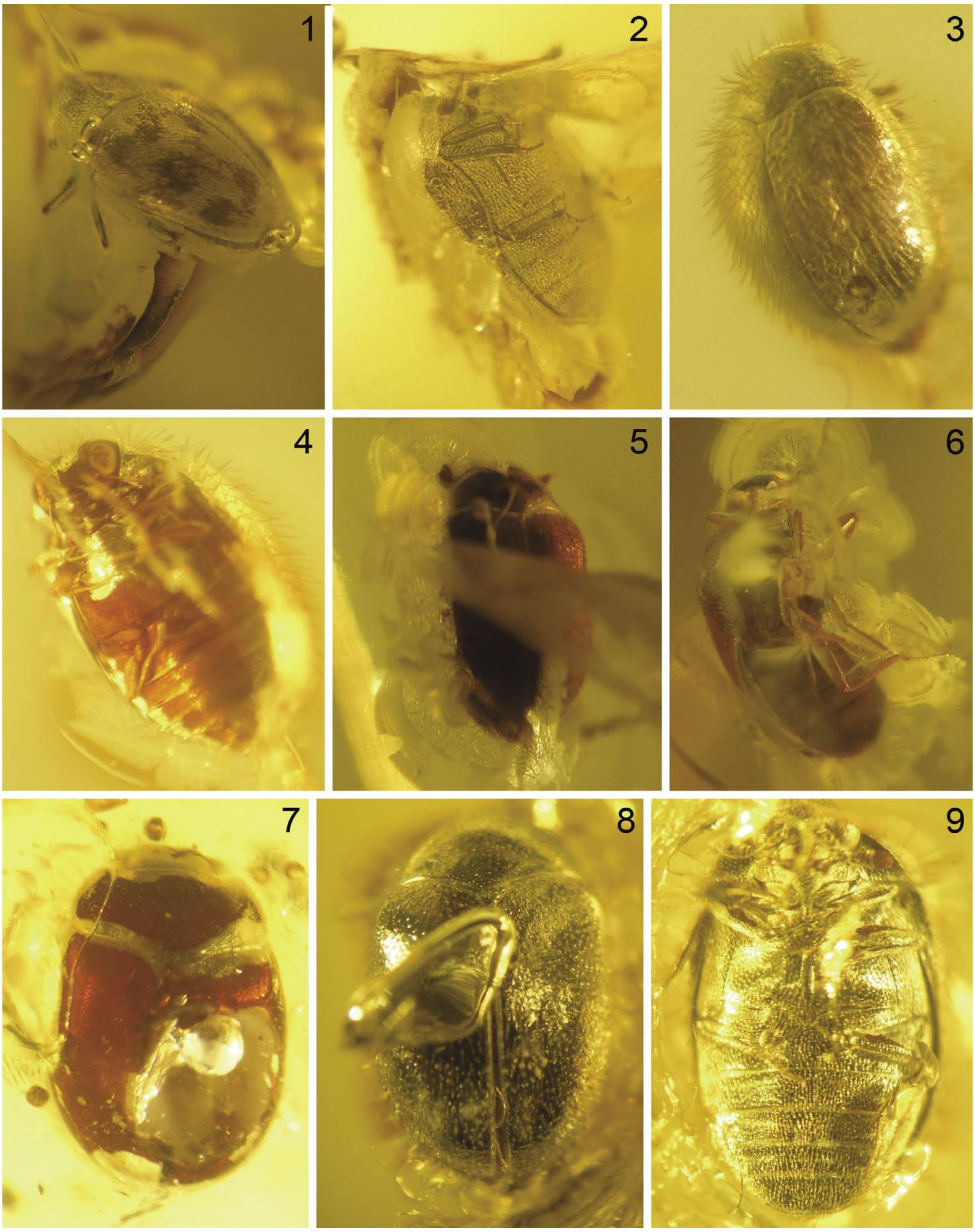
Etymology. Patronymic, dedicated to Friedrich Kernegger (Hamburg, Germany).

***Evorinea amberica* sp. nov.**

(Figs 3, 4, 11)

Type material (holotype). Baltic amber inclusion No. 131/2002, Jantarnyj, Kaliningrad District; Holotype deposited in (GPIH); Holotype specimen is provided with a red, printed label with text as follows: "HOLOTYPE, *Evorinea amberica* sp. nov., J. Háva, J. Prokop & A. Herrmann det. 2005".

Description of holotype. Male. Measurements (mm): TL 1.3 EW 0.8. Head and pronotum dark brown, elytra dark brown, body oval, convex (Figs 3–4). Head dark brown finely punctate with long black erected pubescence. Palpi entirely brown. Frontal median ocellus presented. Antennae 11 antennomerae, antennal club with 2 antennomerae, brown (Fig. 11). Pronotum finely punctate like head with long black erected pubescence; posterior margin without carinae. Scutellum trian-



Figs 1−9. 1, 2 *Anthrenus* (*Nathrenus*) *kerneggeri* sp. nov., holotype, 1 − habitus, dorsal view, 2 − habitus, ventral view. 3, 4 *Evorinea amberica* sp. nov., holotype, 3 − habitus, dorsal view, 4 − habitus, ventral view. 5, 6 *Attagenus balticus* sp. nov., holotype, 5 − habitus, dorsal view, 6 − habitus, ventral view. 7 *Attagenus obesus* sp. nov., holotype, habitus, dorsal view. 8, 9 *Phradonoma ambericum* sp. nov., holotype, 8 − habitus, dorsal view, 9 − habitus, ventral view.

gular finely punctate as pronotum, with short black pubescence. Elytra finely punctate; cuticle unicolorous, dark brown; pubescence black, long, erect. Apex of each elytron with long blackish pubescence. Epipleuron brown with short pubescence. Legs brown with black pubescence. Meso-metasternum with short black pubescence. Posterior margin of metasternum without a small median emargination. Abdominal sternites with short black pubescence. Pygidium brown. Genitalia not visible.

Discussion. The new species belongs to the genus *Evorinea* Beal, 1961 (subfamily Trinodinae: Trinodini) according to characters mentioned by Háva (2004); the genus *Evorinea* contains 10 recent species those differ from new species by the form of antennae.

Etymology. The species named after the English word amber.

Attagenus balticus **sp. nov.**
(Figs 5, 6, 12)

Type material (holotype). Baltic amber inclusion No. 44/1998, Jantarnyj, Kaliningrad District, Russia; Holotype deposited in (GPIH); Holotype specimen is provided with a red, printed label with text as follows: "HOLOTYPE, *Attagenus, balticus* sp. nov., J. Háva, J. Prokop & A. Herrmann det. 2005".

Description of holotype. Measurements (mm): TL 2.5 EW 1.6. Body brown, matt, suboval (Fig. 5). Head dark-brown, finely punctate with very short brown suberected pubescence. Palpi entirely brown. Frontal median ocellus presented. Antennae 11 antennomerae, brown, antennal club 3 antennomerae, dark brown (Fig. 12), terminal segment long. Pronotum dark-brown, finely punctate like head with short black suberected pubescence. Scutellum triangular finely punctate as pronotum, with short black pubescence. Elytra with unicolorous brown cuticle, finely punctate with short subrecumbed pubescence. Apex of each elytron with very short brownish setation. Epipleuron brown, finely punctate, reaching first visible abdominal sternite. Legs entirely light-brown with short brown setation; tibiae without thorns along shaft. Habitus ventral view (Fig. 6). Prosternum not forming a "collar", therefore mouthparts free. Prosternal process narrow. Prosternum coarsely punctate on the disc and foveate on lateral parts. Mesosternum finely punctate as disc of prosternum. Metepisternum foveate punctate,with short brown pubescence. Metasternum finely punctate on the disc and foveate on lateral parts, with short brown pubescence. Abdominal sternites finely punctate, with short subrecumbed brown pubescence. Genitalia not visible.

Discussion. The new species belongs to the genus and nomonotypical subgenus *Attagenus* Latreille, 1802 from the subfamily Attageninae, tribe Attagenini according to characters mentioned by Háva (2004). The new species differs from others known recent species by the form of antennae and form of body. From the Baltic amber known only one recently described species *Attagenus hoffeinsorum* Háva, Prokop et Herrmann, 2006, new species differs from it by the characters mentioned in the following key.

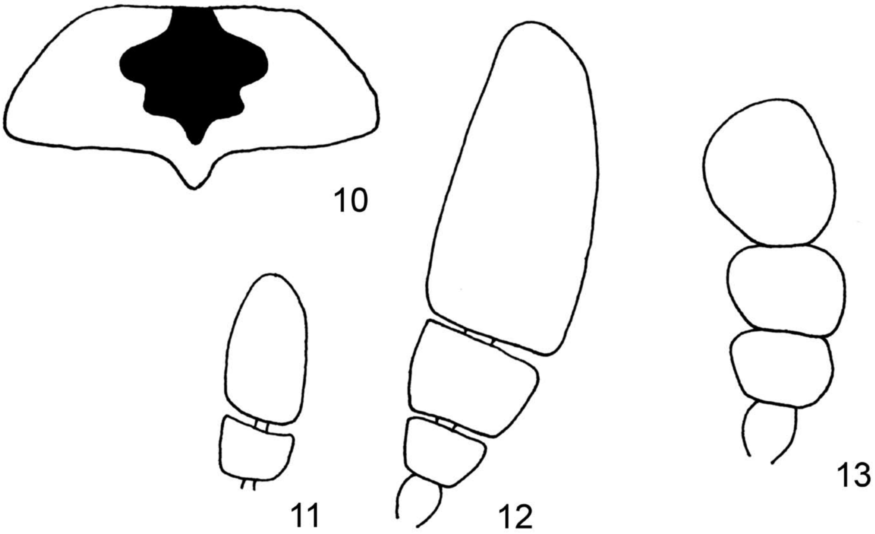
Etymology. The species named after the Baltic amber.

Attagenus obesus **sp. nov.**
(Figs 8, 13)

Type material (holotype). Baltic amber inclusion No. 109/1998, Jantarnyj, Kaliningrad District, Russia; Holotype deposited in (GPIH); Holotype specimen is provided with a red, printed label with text as follows: "HOLOTYPE, *Attagenus, obesus* sp. nov., J. Háva, J. Prokop & A. Herrmann det. 2005".

Description of holotype. Measurements (mm): TL 2.5 EW 1.7. Body brown, shiny, oval. Head brown, finely punctate with very short black suberected setation. Palpi entirely brown. Frontal median ocellus presented. Antennae 11 antennomerae, yellow, antennal club 3 antennomerae (Fig. 13); terminal segment very small, circular. Pronotum brown, finely punctate like head with very short black suberected setation. Scutellum triangular finely punctate as pronotum, with very short black pubescence. Elytra with unicolorous brown cuticle, finely punctate with very short, black, subrecumbed pubescence. Apex of each elytron with very short blackish pubescence. Epipleuron not reaching first visible abdominal sternite. Legs brown with short black pubescence; tibiae without thorns along shaft. Habitus ventral view. Prosternum not forming a "collar", therefore mouthparts free. Prosternal process narrow. Prosternum finely punctate. Mesosternum finely punctate as disc of prosternum. Metepisternum foveate punctate,with short black pubescence. Metasternum finely punctate on the disc and foveate on lateral parts, with short black pubescence. Abdominal sternites finely punctate, with short subrecumbed black pubescence. Genitalia not visible.

Discussion. The new species belongs to the genus and nomonotypical subgenus *Attagenus* Latreille, 1802 from the subfamily Attageninae, tribe Attagenini according to combination of characters proposed by Háva (2004). The new species differs from others known recent species by the form of antennae and body structures. Only one described species from the Baltic amber i.e., *Attagenus hoffeinsorum* Háva, Prokop et Herrmann, 2006 differs from *A. obesus* sp. nov. by the characters mentioned in the following key.



Figs 10–13. 10 – *Anthrenus* (*Nathrenus*) *kerneggeri* sp. nov., holotype, pronotum. 11 – *Evorinea amberica* sp. nov., holotype, antennal club. 12 – *Attagenus balticus* sp. nov., holotype, antennal club. 13 – *Attagenus obesus* sp. nov., holotype, antennal club.

Key to the identification of fossil species of *Attagenus* Latreille, 1802 from the Baltic amber

1(4) elytral epipleuron not reaching first visible abdominal sternite.
2(3) antennae yellow, terminal antennal segment very small, circular (Fig. 13); body oval, cuticle brown, shiny. ....□ *A. obesus* sp. nov.
3(2) antennae black, terminal antennal segment oval; body suboval, cuticle black, matt. .... *A. hoffeinsorum* Háva, Prokop et Herrmann, 2006
4(1) elytral epipleuron reaching first visible abdominal sternite; antennae brown, terminal antennal antennomere long (Fig. 12); body suboval, cuticle brown, matt. .... *A. balticus* sp. nov.

Etymology. Latin adjective obesus = plump, according to a form of the body shape.

Phradonoma ambericum sp. nov.

(Figs 8, 9)

Type material (holotype). Baltic amber inclusion No. 151/2001, Jantarnyj, Kaliningrad District, Russia; Holotype deposited in (GPIH). Holotype specimen is provided with a red, printed label with text as follows: “HOLOTYPE, *Phradonoma, ambericum* sp. nov., J. Háva, J. Prokop & A. Herrmann det. 2005”.

Description of holotype. Measurements (mm): TL 2.4 EW 1.5. Body black, shiny, covered with black long erected pubescence (Fig. 8). Head black, finely punctate with distinct erected setation. Palpi entirely brown. Frontal median ocellus presented. Antennae with 11 antennomerae, black, antennal club 3 antennomerae, terminal antennomere oval (Fig. 9). Antennal cavity open. Pronotum finely punctate like head with long black erected pubescence. Scutellum triangular finely punctate as pronotum, with very short black pubescence. Elytra coarsely punctate near scutellum, finely punctate on other parts; cuticle unicolorous, black, with black erected long pubescence. Apex of each elytron with long pubescence. Epipleuron black, with long black pubescence. Ventral surfaces as in (Fig. 9). Prosternum forming a “collar” under which mouthparts fit when head is retracted, with coarsely punctures. Epipleuron reaching of anterior ½ episternum. Mesosternum and metasternum covered with black very short recumbed pubescence. Metasternum at lateral part near epipleuron with foveate-reticulate punctures. Abdominal sternites finely punctate, covered with black very short recumbed pubescens. Legs black, with short black setation; antrior tibiae with spines along shaft. Genitalia not visible.

Discussion. The present described species belongs to the genus *Phradonoma* Jacquelin du Val, 1859 according to the number of antennomeres and short spines along shaft on anterior tibiae. The genus *Phradonoma* attributed within the genera Group II according to the genera keys proposed by Háva (2004). The genus comprises 40 recent species and our species belongs into „*P. villosulum* species group“ defined by Háva (2006) differing by the form of antennae.

Etymology. The species named after English word amber.

Attagenus hoffeinsorum Háva, Prokop et Herrmann, 2006

Material examined. Five inclusions in Baltic amber, Nos. 37/1992, (FKHC); 278/1994, (FKHC); 44/2003, (FKHC); 103/2003, (FKHC); 109/2003, (JHAC); Jantarnyj, Kaliningrad District, Russia.

Remarks. The species known according to the type series, from Poland mentioned by Háva et al. (2006), additional specimens from Baltic amber is clearly attributable to this species.

Anthrenus (*Nathrenus*) *ambericus* Háva, Prokop et Herrmann, 2006

Material examined. One inclusion in Baltic amber No. 45/2000 (FKHC), Jantarnyj, Kaliningrad District, Russia.

Remarks. Additional specimen from the Baltic amber is clearly attributable to this species.

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Authors are indebted to Friedrich and Barbara Kernegger (Hamburg, Germany) who kindly loaned us an interesting amber material of dermestid beetles. The second author (JP) acknowledges the research support from the Grant Agency of the Czech Republic No. 205/08/0643 and Ministry of Education MSM 0021620828.

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Demography of *Bufo bufo* (Amphibia: Anura) in the Strnady breeding pond, Czech Republic

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Abstract. Changes of common toad's *Bufo bufo* (Linnaeus, 1758) numbers in breeding pond, survival rate, breeding season skipping and the population age structure and age of sexual maturity based on skeletochronology method was studied in Strnady, Czech Republic (N 49°56'34.6"; E 014°23'23.8"; 233 m a.s.l.) during 1991–1995 period. The most numerous age categories in breeding pond were six and five years for males and six years for females. Average age was 5.2 years for males and 5.5 years for females. Males arriving to breeding pond already in amplexus were significantly older than males arriving solo. Correlation between snout-went lenght (SVL) and age was low for both sexes. No any relation between male's and female's age in pairs was detected nevertheless there was significant tendency of older males to arrive later on. Males mature in the age of 2–6 years, females in the age of 3–6 years. Correlation between SVL and age of newly matured males was not significant. Approximately 1/3 of males and females is refreshing breeding agregation every year. Survival rate of males marked in 1991 was following during succeeding years: 48.5%, 25.8%, 9.9% and 3.2%. Survival rate of females was following: 37.5%, 18.9%, 5.7% and 1.9%. On average, males were participating in more breeding seasons (1.87) than females (1.64). Skipping of one or more breeding season(s) was quite common, especially for females. Nevertheless some individuals of both sexes arrived to breeding pond five years without interruption.

Demography, mortality, survival rate, reproduction cycle, abundance changes, sexual maturity, age structure, Central Bohemia

INTRODUCTION

Common toad *Bufo bufo* (Linnaeus, 1758) is potentially long-living animal. Smith (1951) mentioned forty years nevertheless standard situation in natural conditions is quite different. Maximum age of common toad was 9 years (Kuhn 1994) and 9–12 years relating to locality (Gittins et al. 1985, Hemelaar 1986). Individuals from colder climate (higher altitude or latitude) are living longer than animals from warmer areas. Surviving is more important for whole-live reproduction success than competition in breeding pond. Elder females profit from better breeding conditions (more or bigger eggs). According to Kuhn (1994) most of females is laying eggs only once per life and only 5–25% of females breed more than once (maximum was five times per life). Reading's (2001) estimate is slightly more optimistic – average survival rate was 31.9% (12.3–52.7%) for males resp. 16.7% (6.9–37.3%) for females in south England. Hodrová (1975) mentions arrival of 45% (40.6–50.8%) males and 35.9% (28.0–54.5%) females in following season and Obrmajer (1985) mentions arrival of 45.13% males and 33.93% females in following season from the same locality (central Bohemia). Nevertheless these data do not take into account individuals skiping one or more seasons. According to Frazer (1966) only 11% of common toads will arrive third year back to breeding pond. Winter climate conditions seem to be most important abiotic factor affecting mortality of anurans over-wintering out of water (Elmberg 1990).

The absence of any individual toad in breeding pond in following season is not inevitable signalising its death. Skipping of one or more reproduction season(s) is well documented for common toad. Annual ovarian cycle of females is prevailing in some populations (Frazer 1966, Hede 1976, Wisniewski et al. 1980, Hemelaar 1986, Jörgensen et al. 1979, Gittins 1983) nevertheless in other populations skipping of some season(s) by females is dominating (Heusser 1968, Hede & Jörgensen 1978). This phenomenon is stronger for females comparing with males also in frame of the same population (Hemelaar 1986, Kuhn 1994). Reproduction is energetically exhausting and successful breeding period can not follows to bad feeding period of previous year. Skipping of one or more breeding period(s) is reproductive adaptation to worsen living conditions – either individual (non-sufficient fat supplies) or influencing all population (high altitude or latitude=short feeding period) (Bull & Shine 1979).

Body dimensions are generally considered to be non-sufficient reflection of anuran age. It is true that Hemelaar (1983, 1985) found tendency of bigger common toads to be also elder nevertheless body dimensions are non-sufficient for more exact age determination (Hemelaar 1996). The biggest toads are not necessarily also the oldest ones and individuals growing slowly and gradually are mostly long-living ones (Castanet & Smirina 1990, Smirina 1983). Differences in body dimensions among toads of the same age class are getting bigger with age growing (Reading 1988). According to Wind-Larsen & Jörgensen (1987) age determination of common toads smaller than 60 mm or lighter than 20 g is not possible.

Also Halliday & Verrell (1988) mentioned that bigger body dimensions of common toad males reflect their quicker growth rather than higher age. Growing pace could be influenced also genetically as it was showed for another anuran species (Emlen 1976, Wilbur et al. 1978, Woodward 1986, Woodward et al. 1988). At the other side Cooke & Oldham (1995) found significant correlation between age and snout-went lenght (SVL) for common toad males but not for females.

There are differences among populations in age structure nevertheless the youngest category in breeding pond is not being the most numerous. Usually animals of middle age category are the most numerous (Hemelaar 1986). According to Smirina (1983) such category was created by 3–4 years males and 4 years females.

Age structure of common toad breeding part population differs among years. Result of breeding period two to three years ago and surviving rate of newly metamorphosed toads are affecting such differences.

Start of sexual maturity of common toads is relating to age, body size and season of year (Jörgensen 1988). Climate conditions and food availability are key factors (Jörgensen et al. 1978, Jörgensen 1984). Maturation is put off and toads mature in bigger body size in areas with shorter feeding period (higher latitude or altitude). Males mature earlier than females (Hemelaar 1986).

Whether summer period of aestivation in warmer areas will also affect start of maturation is questionable. Shorter winter period will probably compensate summer period of inactivity in these areas as it was observed by Caetano (1990) for newts *Triturus boscai* (Lataste, 1879) and *T. marmoratus* (Latreille, 1800).

It is general for temperate amphibians that some minimal body size has to be achieved before sexual maturation is reached (Ryan 1983, Flindt & Hemmer 1970, Hede 1976, Hede & Jörgensen 1978, Glandt 1981, Gibbons & McCarthy 1984) and such body size limit is decreasing with age growing of individual (Kuhn 1994). Body size of common toad is much better indicator of maturity than age and maturation of the same spring hatchlings will not be necessary equal (Jörgensen & Billeter 1982, Reading 1988, Smirina 1983). Gittins et al. (1982) found no any correlation between body size and age of common toad in moment of sexual maturation.

Reaching of sexual maturity is followed by strong slow down of growth of both sexes (Smirina 1983, Jörgensen 1986, Kuhn 1994). Energy from food is used mainly for reproduction and surviving after reaching of sexual maturity (Hemelaar 1986). Nevertheless very limited growth is continuing till the fifth year (Hemelaar 1986).

Till age of two years when dramatic slow down of male growth occurs no any differences in body size of males and females exist (Smirina 1983). Because females reach maturity later on their growth is continuing longer. Growth could continue in years when females are not reproducing (Hemelaar 1986).

95% of males presented in breeding pond were bigger than 51 mm (SVL of the smallest male was 42 mm) and 95% of females were bigger than 62 mm (SVL of the smallest female was 51 mm) in Holland. Hemelaar (1986) consider these values to be limit of sexual maturation valid for this locality. According to Jörgensen et al. (1979) females are reaching sexual maturity in 62–80 mm and/or 30–65 g in Denmark.

It is possible to speculate about minimal age limit of sexual maturation because growth of common toads is continual during all period of activity nevertheless reproduction occurs only one times per year. So age limit could reflect number of years indispensable for reaching of body size sexual maturity limit.

Males of common toad mature before females. The youngest females in reproduction pond are at least one year elder than the youngest males (Hemelaar 1986). Males tend to enter breeding aggregation as soon as possible but selection prefers delayed maturation of females because their body size is strongly correlated with their fertility or size of eggs (Hemelaar 1986).

Age of the youngest females in breeding pond was 3 years (Kuhn 1994), 4–5 years and no less than 3 years (Hemelaar 1983, Reading et al. 1991, Gittins et al. 1982) or 4 years (Smirina 1983). Nevertheless some females reach maturity much later – 7 years (Kuhn 1994), 8 years (Gittins et al. 1982, Gibbons & McCarthy 1983) and 9 years (Hemelaar 1983). Age of the youngest males taking part in breeding aggregation was 2 years (Gittins et al. 1982, 1985, Hemelaar & van Gelder 1980, Hemelaar 1981, 1983, Smirina 1983, Reading 1988, 1991) nevertheless most of them enters breeding pond for the first time in age of 3–4 years or 5–6 years relating to locality (Hemelaar 1983, Reading 1988) and some of them in age of 8 years.

METHODS

Enclosing of breeding pond by plastic fence and placing of pit-fall traps around fence was the method of common toad catching during five breeding period 1991–1995 in Strnady, Central Bohemia (49° 56’ N; 14° 23’ E; 233 m a. s. l.). Traps were controlled daily in the morning from the moment of pond enclosing till fence removing in the end of migration period. Toads were removed from traps continually in days with migration culminating. Individuals trying to abandon enclosed area were released out of fence. Peoples living near of pond were informed about research not to negatively influence project.

Information about presence and mortality/survival rate of toads is based on marking (toe clipping) of all migrating toads during five successive years without interruption. End of the same toe was cut off each year to all toads (marking was not individual). Toe clipping is the most common method of amphibians marking (Martof 1953, Reading & Clark 1983, Gittins et al. 1980). Nevertheless some authors mention that toe-clipping cause lost of blood (Noble 1954, Clark 1971) and Joly & Miaud (1990) and Clark (1972) mention reduction of mobility by clipping of two and more toes. Regeneration rate of clipped anuran toes is not significant comparing with newts and salamanders.

Subsequent casual control of animals in water was aimed to eliminate penetration of non-marked animals into pond. Analysis of toads´ numbers during five successive seasons is based on complete account of all individuals arriving to breeding pond. This method allows to distinguish animals skipping of some breeding season(s) from dead ones. The term “surviving” involves animals participating in breeding aggregation and animals skipping of breeding season but still living and participating in some of following breeding seasons as well. Values from first years are probably slightly underestimated.

Because no toad was omitted during migrations and five years was quite enough to afflict vast majority of “skipping” animals this method also allowed to get a picture about life-long pattern of reproduction partitioning – rate of “skipping”. Absence of any other suitable breeding place in broad surrounding area (locality is bordered by fast running big Vltava river, steep rocks and big spruce forests) makes a switch between tha study breeding pond and other ponds impossible for toads.

Age of toads was analysed by skeletochronology (Smirina 1972a, b, Hemelaar & van Gelder 1981, Hemelaar 1985, 1986). Detail description of this method and review of approaches used by different authors is summarised in Kovář (1999). Last but one phalanx of second digit from left hind limb was used for analysis in 1995.

Phalanx cutting was used also for toads marking. Blood supplying of peripheral parts of limbs is probably reduced in cold conditions. This procedure did not seem to be too stressful and toads did not loose any blood. 26 males and 9 females were randomly selected for analysis.

Cut phalanxes were immediately placed into 90% alcohol. Using paraffin microtone series of fifteen samples (15 µm thin) were cut from each digit bone in the middle of phalanx. Marrow cavity is the narrowest here. Cut slices were coloured by haematoxylin method used in human dentist research. Details of bone slices colouring and growing lines counting are presented in Kovář (1999).

Number of growth rings was counted in light microscope. Correction for excluding of resting lines ressorption effect was done according to methodology described by Hemelaar (1986).

The same skeletochronological analysis provided data also for studying of minimal age corresponding to sexual maturity. Because all toads arriving to breeding pond were marked also in previous four years, age corresponding to first reproduction of all toads analysed by skeletochronolog was easy do describe by back counting.

Individuals of both sexes arrived to breeding pond for the first time without marks in 1995 after previous four years of marking of all toads were considered to be newly matured and their SVL was considered to be limit of maturity.

RESULTS

Figure 1 presents population abundance changes during period 1991–1995. Decreasing of population density was stronger for males (22.2%) than for females (33.4%). Especially sharp decline occurred between 1992 and 1993. Only 46.5% of males and 79.4% of females arrived. Influences affecting differently to both sexes were probably responsible for unequal density decrease. Although density was declining during all five years of study period this process did not escalate (Fig. 2).

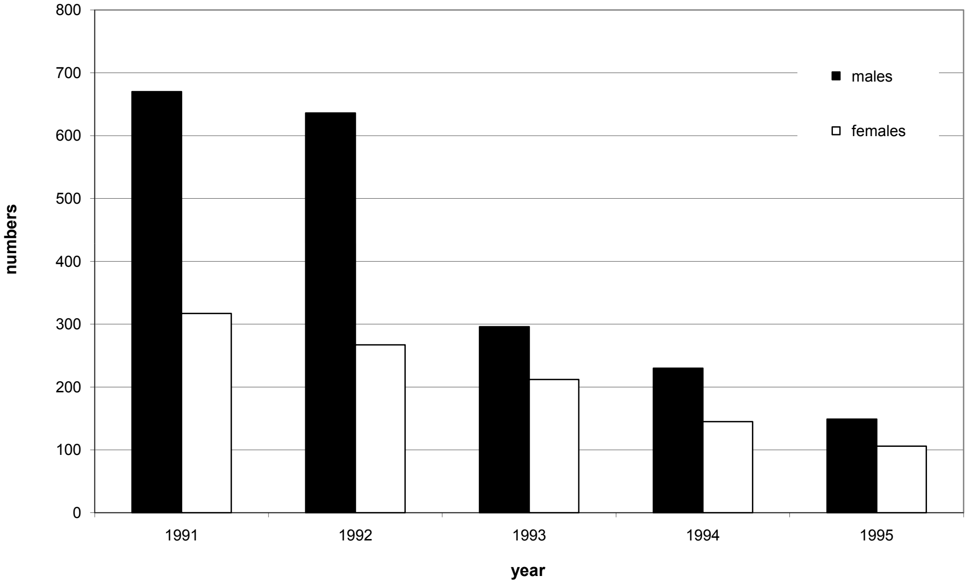

Fig. 1. Total numbers of toads arrived to breeding pond during five study years.

Table 1. Survival of males and females marked in 1991 for the first time

	1991		1992		1993		1994		1995	
	inds	%	inds	%	inds	%	inds	%	inds	%
males	670	100	325	48.5	173	25.8	66	9.9	22	3.2
females	317	100	119	37.5	60	18.9	18	5.7	6	1.9

Table 1 presents numbers of surviving toads firstly marked in 1991. Based on the Table 1 probability of surviving till sixth season seems to be extremely low for both sexes. Males are participating in 1.87 breeding seasons and females in 1.64 breeding seasons on average. This difference is statistically significant (P<0.05).

Approximately half of males had not survived from first to second and from second to third year and than mortality has raised to approximately 2/3 from third to fourth and from fourth to fives year. Mortality of females was more stable among years except of situation between first and second year.

Skipping of one or more breeding season(s) was quite common phenomenon in Strnady population. It was more often for females (P<0.01, based on the chi-squared test domparing to relative frequencies) than for males. On the contrary some individuals of both sexes visited breeding pond every year without skipping. Female's tendency to visit breeding pond every year without skipping was weaker comparing with males nevertheless this difference was not statistically significant (P>0.05, based on the chi-squared test domparing to relative frequencies). 1.3% of females and 1.8% of males arrived to breeding pond in 1995 had taken part already in four previous breeding seasons without interruption. In course of five study years nearly all possible combinations of one or more breeding season(s) skipping were detected (see Fig. 3). One male marked in 1991 skipped even three seasons and came back in 1995.

150 (86.7%) males from 173 marked first in 1991 and surviving till 1993 (no matter whether they arrived or not in year 1992) were present in breeding pond also in 1992 and 23 (13.3%) males skipped this season. 35 (52.2%) males from 67 ones firstly marked in 1991 and surviving (no matter whether they arrived or not) till 1994 were present in breeding pond during both previous seasons (1992 and 1993) and 22 (32.8%) males skipped only 1993 season, 2 (3.0%) males skipped only 1992 season and 8 (12.0%) males skipped both seasons.

This analysis shows prevailing tendency of males to visit breeding pond yearly. 38 (63.3%) females from 60 ones firstly marked in 1991 and surviving (no matter whether they arrived or not) till 1993 were present in breeding pond also in 1992 and 22 (36.7%) females skipped this season.

8 (44.4%) females from 18 ones firstly marked in 1991 and surviving (no matter whether they arrived or not) till 1994 were present in breeding pond during both previous seasons (1992 and

Table 2. Between year changes of mortality of toads firstly marked in 1991

	males		females	
year	survival rate	mortality	survival rate	mortality
1991	670		317	
1992	325 from 670	51.5%	119 from 317	62.5%
1993	173 from 325	46.8%	60 from 119	49.6%
1994	66 from 173	61.8%	18 from 60	70.0%
1995	22 from 66	66.7%	6 from 18	66.7%

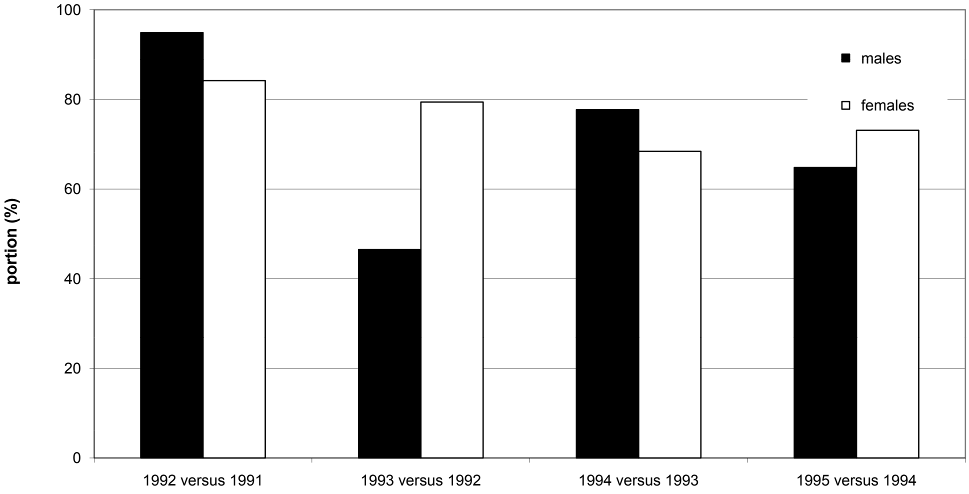

Fig. 2. Population density changes between various years.

1993) and 2 (11.1%) females skipped only 1993 season, 3 (16.7%) females skipped only 1992 season and 5 (27.8%) females skipped both seasons. Female's tendency for skipping of some breeding season(s) is stronger.

Table 3 is summarising above mentioned results for both sexes. Composition of males regarding to number of breeding seasons taken part after five years of marking was as follows in 1995: 28.7% for the first time, 39.2% for the second time, 8.4% for the third time, 15.4% for the fourth time and 8.4% for the fives time. Newly matured males refreshed approximately 1/3 of breeding population in 1995.

Table 3. Result of absent/present analysis in the Strnady breeding pond during five successive breeding seasons; legend: 1 = present, 0 = absent

		year			n	
1991	1992	1993	1994	1995	males	females
1	1	1	1	1	12	4
1	1	1	1	0	22	4
1	1	1	0	1	1	0
1	1	1	0	0	93	28
1	1	0	1	1	5	2
1	1	0	1	0	17	0
1	1	0	0	0	152	59
1	0	1	1	1	2	0
1	0	1	0	0	13	14
1	0	1	1	0	0	3
1	0	0	1	1	1	0
1	0	0	1	0	6	5
1	0	0	0	1	1	0
1	0	0	0	0	345	198

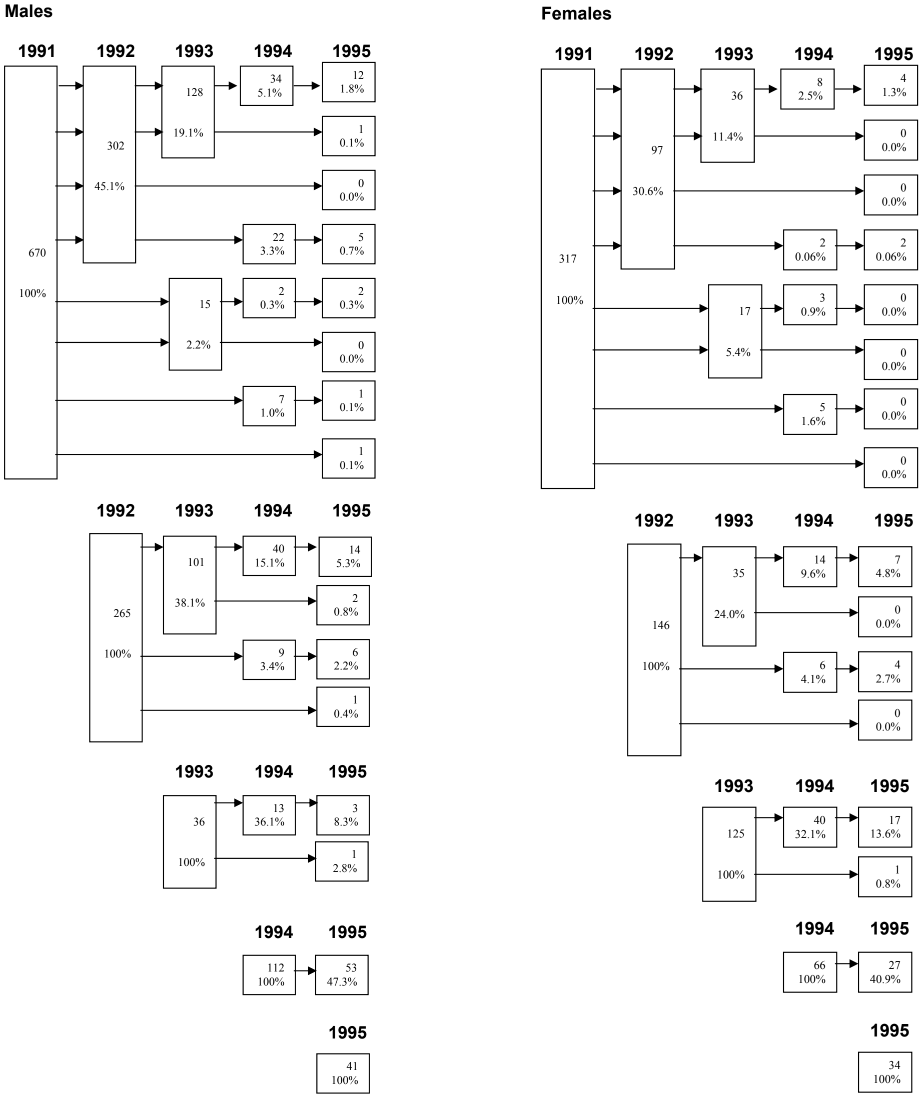

Fig. 3. Arrivals of toads to breeding pond during five successive years. Only individuals with clear evidence of year marks are included into analyses.

Composition of females regarding to number of breeding seasons taken part after five years of marking was as follows in 1995: 35.4% for the first time, 29.2% for the second time, 21.9% for the third time, 9.4% for the fourth time and 4.2% for the fives time. Newly matured females refreshed approximately 1/3 of breeding population in 1995.

Table 4 summarises demographic data used for skeletochronological analysis about breeding part of population in 1995. Figure 4 shows age composition in breeding pond. Six and five years

Table 4. Age, SVL, date of arrival to breeding pond and partner in amplexus before water entering; legend: SVL = snout--went lenght; SA = skeletal age; SA1 = skeletal age at the first breeding season

Ind. No.	partner in amplexus	date	participation in breeding season	SVL [mm]	SA	SA1
males						
1	solo	18.03.95	94, 95	74	4	3
4	solo	25.03.95	95	76	5	5
5	solo	25.03.95	94, 95	79	4	3
6	solo	25.03.95	95	75	4	4
7	solo	25.03.95	95	69	4	4
8	solo	25.03.95	95	71	5	5
15	solo	27.03.95	95	66	4	4
16	solo	27.03.95	95	67	4	4
18	solo	27.03.95	94, 95	72	5	4
21	solo	27.03.95	95	70	5	5
22	solo	27.03.95	95	67	5	5
40	female No. 41	04.04.95	92, 93, 94, 95	72	7	4
42	female No. 43	04.04.95	94, 95	71	5	4
44	solo	04.04.95	94, 95	?	5	4
46	solo	04.04.95	92, 94, 95	70	6	3
47	female No. 48	04.04.95	92, 95	69	5	2
49	female No. 50	04.04.95	95	70	6	6
51	solo	04.04.95	91, 92, 93, 94, 95	74	6	2
52	female No. 53	04.04.95	91, 92, 93, 95	76	6	2
54	solo	04.04.95	91, 92, 93, 94, 95	69	6	2
70	female No. X	04.04.95	91, 92, 93, 94, 95	70	6	2
71	female No. X	04.04.95	91, 92, 94, 95	69	6	2
72	female No. X	04.04.95	91, 95	?	6	2
74	female No. X	04.04.95	91, 92, 93, 94, 95	76	6	2
90	female No. 91	06.04.95	91, 92, 93, 94, 95	78	6	2
94	solo	06.04.95	92, 94, 95	73	5	2
females						
41	male No. 40	04.04.95	94, 95	98	4	3
43	male No. 42	04.04.95	95	89	4	4
45	solo	04.04.95	95	73	5	5
48	male No. 47	04.04.95	92, 93, 94, 95	92	6	3
50	male No. 49	04.04.95	92, 94, 95	97	6	3
53	male No. 52	04.04.95	93, 94, 95	92	5	3
73	solo	04.04.95	91, 92, 94, 95	?	7	3
91	male No. 90	06.04.95	95	98	6	6
96	solo	06.04.95	94, 95	95	6	5

males were the most numerous age categories in breeding pond followed by four years and seven years males. Average age of males in breeding pond in 1995 was 5.2 years (n=26).

Six years females created the most numerous age category followed by nearly equally numerous four and five years categories. Seven years females created the least numerous age group. Average age of females in breeding pond was 5.5 years (n=9).

Comparing of identical male and female age categories, elder females seem to be more numerous nevertheless between-sexes difference in average age is not significant (P>0.05, Student t-test). Because age of only nine females was analysed power of test is not too strong. Males arriving to breeding pond already in amplexus (5.8 years, n=11) were significantly (P<0.01) elder than males (4.8 years, n=15) arriving solo (Student t-test).

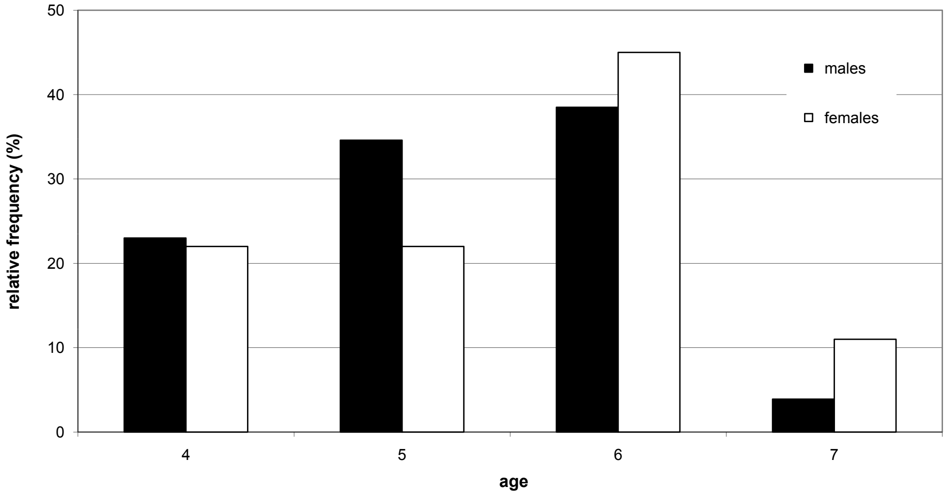

Fig. 4. Males' and females' age categories in Strnady breeding population in 1995.

Average SVL of four years males was 71.67±5.13 mm, five years males was 71.13±2.70 mm, six years males was 72.4 ± 10.00 mm and one seven years old male measured 72.00 mm. Correlation of SVL and age was low for males (r=0.05, n=25) and for females (r=0.22, n=8) as well. Therefore, based on these data, it is not possible to determine age of toads from their SVL. Based on analysed data sample no relation between male's and female's age in pairs was detected (n=6, r=0.23). Positive relation between male's age and date of arrival to breeding pond was determined

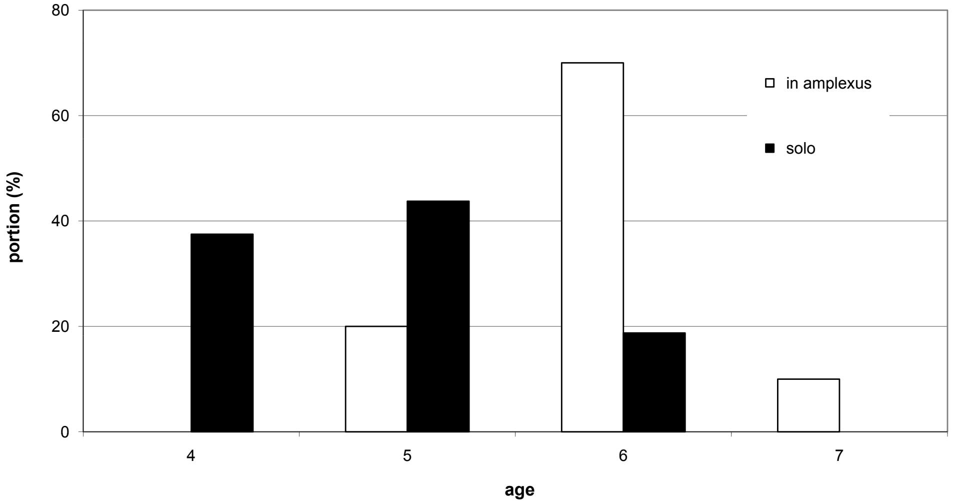

Fig. 5. Composition of males' age categories arriving solo and in amplexus.

Table 5. Age of newly matured toads (arrived to the breeding pond for the first time in 1995)

age [years]	males		females	
	n	%	n	%
2	10	38.5	0	0.0
3	2	11.5	5	55.6
4	8	30.8	1	11.1
5	4	15.4	2	22.2
6	1	3.8	1	11.1

(n=26, r=0.77). Clear tendency of elder males to arrive later on is visible from Fig. 6. SVL of the smallest male was 52 mm and the smallest female was 75 mm in breeding pond, nevertheless 95% of males were bigger than 61 mm and 95% of females were bigger than 81 mm. These SVL limits probably reflect level of sexual maturation. Correlation between SVL and age of newly matured males was not significant, only nine males was analysed, however.

DISCUSSION

Observed population abundance declining during five years could be caused by growing mortality, growing rate of breeding season skipping, changing of breeding pond by migrating toads or non-sufficient refreshing of breeding population by newly matured toads. Common toad has strong fidelity to its natal breeding pond and there is no other suitable breeding place near the Strnady pond. Biometrical analysis showed that big toads did not disappear from population significantly but number of small toads was decreasing there. Statistically significant shift in breeding popu-

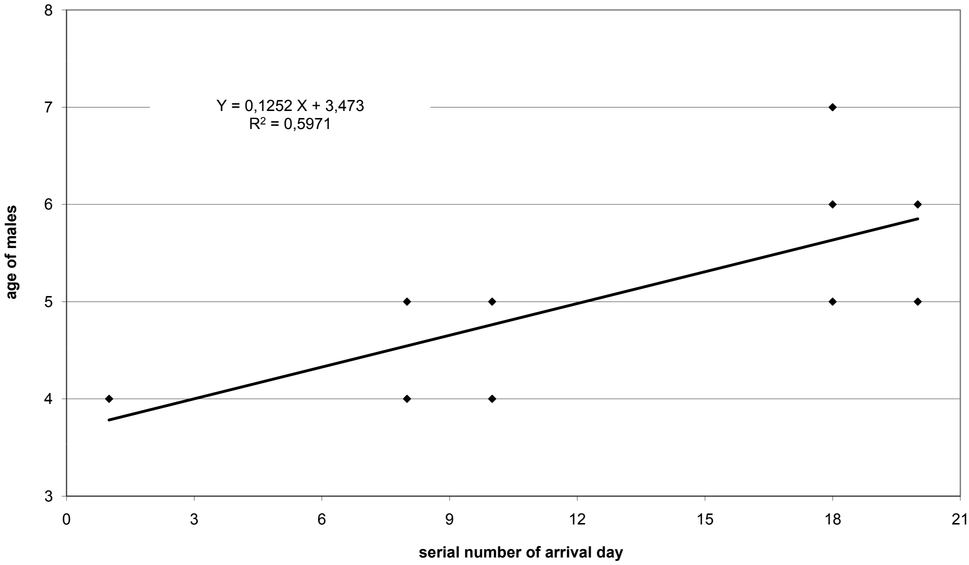

Fig. 6. Correlation between age and date of males arrivals.

lation towards bigger body dimensions (stronger for males) probably reflects decreasing rate of newly matured toads caused probably by problems in breeding pond a few years ago. Such very bad breeding season was observed a few years later in 1997 when only a very limited number of small toads metamorphosed in Strnady.

General survival rate was much better in Strnady comparing with Kuhn (1994) mentioning that only 5–25% of females take place in more than one breeding season and with Frazer (1996) mentioning that only 11% of common toads will arrive following year as well. Also average survival rate mentioned by Reading (2001) – 31.9% for males resp. 16.7% for females is much lower. Mortality of females did not change in Strnady with ege growing nevertheless such a change was visible for males (mortality was growing with males´age).

Five breeding seasons as a maximum per life in Strnady is identical with finding of Kuhn (1994) and Reading (2001).

Both populations with yearly pattern of reproduction (Frazer 1966, Hede 1976, Wisniewski et al. 1980, Hemelaar 1986, Jörgensen et al. 1979, Gittins 1983) and populations characterised by common skipping of breeding seasons mainly by females (Heusser 1968, Hede & Jörgensen 1978, Daugherty & Sheldon 1982) are documented in frame of common toad area of distribution.

Neither regular breeding seasons skipping nor yearly visiting of breeding pond is typical breeding strategy of common toad population living under climatic and food conditions of Strnady. Nevertheless tendency to visit breeding pond every year is stronger for males comparing with females. This phenomenon probably reflects bigger energetic demands connected with reproduction of females. The same difference between sexes found Hemelaar (1986) and Kuhn (1994). Climatic conditions of previous feeding season and individual ability to cumulate sufficient energy supplies determine rate of skipping/arriving animals. Absence of any clear reproduction cycle pattern in Strnady population probably reflects average living conditions in frame of species area of distribution.

Regarding to mortality/surviving rate and intensity of “skipping” described during five successive years it was possible to recognise with high accuracy animals arriving to breeding pond for the first year (newly matured) in 1995. Recruitment rate determined in 1995 (28.7% of males and 35.4% of females) is not probably stable value and will strongly fluctuate among years related to breeding success in previous seasons (number of eggs laid, number of metamorphosed young toads) and surviving rate of young toads till maturation. These figures are much lover comparing with data mentioned by Reading (2001). Inexperienced (first breeding) males and females in his 20 years study always far outnumbered (males 56.3–91.2%, females 71.7–93.6%) experienced ones.

Skeletochronology is a useful method for age determination of animals with whole-life growth living in climate regime with annual metabolic activity fluctuation. Different intensity of bony tissue growth is visible in cross sections of digits phalanxes. Quality of microscopic samples preparation and experience of person counting growth rings are crucial for right age determination. Especially decreasing of distance between growth rings (Castanet et al. 1988, Hemelaar 1981) with age continuing complicates analysis.

Possible underestimation of age was limited by complete capturing and marking of all individuals migrating to Strnady breeding pond in previous four years. So information about previous arrivals was available for each analysed individual.

Data from Strnady are in agreement with Hemelaar (1986) and Kuhn (1994) mentioning that body dimensions are non-sufficient for correct age determination. Differences in body dimensions among individuals of the same age are getting bigger with age growing.

Lower and upper age limits of males and females participating in breeding aggregation in Strnady are comparable with German localities (Hemelaar 1986) and age composition of females is comparable as well. The most numerous male's age group was six years in Strnady comparing with four years mentioned by Hemelaar (1986) from German locality. Age composition of populations from France and Holland did not differ too much from Strnady but males and females from Sweden and Norway were elder on average.

Age of the oldest females mentioned from German locality by Kuhn (1994) was 9 years from Strnady only 7 years.

Non-significant difference in average age of males (5.2 years) and females (5.4 years) in Strnady is in agreement with whole-life number of reproduction seasons. Slightly higher average number of whole-life reproduction of males (1.87) comparing with females (1.64) is caused by earlier sexual maturity. Nevertheless age of only nine females was analysed.

Finding that elder males are arriving to breeding pond paired significantly more often than younger ones is interesting nevertheless analysed sample was small and is covering only one year. There are no any comparable data from other studies.

Age related timing of males' arrivals to breeding pond (delayed arrival of elder males), described from Strnady in 1995 is the same case. This phenomenon could reflect either age-related breeding strategy of males or more remote located summer home ranges of elder males.

Because all arriving toads were marked completely in five successive years (1991–1995) it was possible to recognise newly matured individuals in last year of analysis with high level of accuracy. In accordance with other authors males reach sexual maturity and enter breeding aggregation in lower age than females also in Strnady. Minimal age (males – 2 years, females – 3 years) of sexual maturity in Strnady is corresponding to other area of distribution (Gittins et al. 1982, 1985, Gibbons & McCarthy 1983, Hemelaar 1981, 1983, Kuhn 1994, Hemelaar & van Gelder 1980, Smirina 1983, Reading 1988, 1991). Nevertheless toads from Sweden and Norway are starting with reproduction in higher age Hemelaar (1986).

Some individuals reach sexual maturity later on and age composition of newly matured toads is not stable between years and localities as well. Nevertheless, it seems to be a general tendency that toads of both sexes reaching maturity after sixth year of live are an exception. In Strnady breeding pond 96.2% of males and 88.9% females reached maturidy till fifth year of live resp. 80.8% of males and 66.7% of females reached maturidy till fourth year of live.

Body size limit of sexual maturity is not stable value and differs among localities. This value was much bigger for both sexes in Strnady comparing with study of Hemelaar (1986) in Holland and similar with situation in Denmark (Jörgensen et al. 1979).

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Reproduction strategy of *Bufo bufo* (Amphibia: Anura) in the Strnady breeding pond, Czech Republic

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Abstract. Reproduction strategy, sex ratio, influences, course and duration of migration and whole breeding period of common toad's *Bufo bufo* (Linnaeus, 1758) were studied during 1991–1995 period in Strnady, Czech Republic (49° 56' N, 14° 23' E; 233 m a. s. l.). Migration of toads started always till middle of March and usually continued till April. The beginning of toads' activity corresponds to first longer period of warmer spring weather. Migration is commonly interrupted by cool periods. Migration took 32 days on average, but only 18 days on average when considering only days/nights with appropriate temperature. Duration of total reproduction period was 36 days on average. Average night temperature bellow 2 °C is not sufficient for migration of any sex. Average night temperature around 4 °C is quite sufficient for males. Females usually respond only to slightly higher temperature. Highly male biased sex ratio at the beginning of migration was getting corrected after night(s) when main wave of migrating toads reached pond. Relating to season sex ratio in breeding pond was fluctuating between 3.1 and 1.4 from this moment till mass eggs laying. Sex ratio in the beginning of mass eggs laying was between 1.4 and 2.8, total sex ratio was between 2.4 and 1.4 and average operating sex ratio was between 2.1 and 3.4 according to season. Males had the best chance to get females already in dry land during main migration waves. Nearly all females migrating out of main migration waves were paired before water entering. Males had 5, 23, 30, 6 and 6 days in particular seasons to compete each other till beginning of mass oviposition. There was no any consistent among years relation between male's SVL and time of their water entering and no any tendency of bigger or smaller males to synchronise their arrival with main migration wave(s) of females as well. There was tendency of lighter males to arrive sooner than heavier ones. Males arriving to water already paired were significantly bigger than males arriving solo and significant positive correlation between SVL of males and females in pairs already before water entering existed.

Reproduction strategy, sex ratio, pairing, breeding success, migration, male-male competition, reproduction, Central Bohemia

INTRODUCTION

One breeding season is typical for common toad, nevertheless Hemelaar (1986) described population from France with two periods of eggs laying. Annual rhythm of common toad *Bufo bufo* (Linnaeus, 1758) is controled mainly by climate conditions, but internal timer could play role as well (Jörgensen 1983). According to Sinsch (1988) temperature in hibernation shelters of common toads fluctuate from 0.9 °C till 3.1 °C also during hard frosts. Growing of temperature to 14 °C in winter period will not trigger leaving of hibernation shelters. Common toads are responding to temperature fluctuation by vertical movement (relating to temperature and type of hibernation shelter from 0 till more than 0.8 m). Body temperature of most buried toads was the highest (3.3 °C). The lowest body temperature was 0.6 °C (van Gelder et al. 1986).

According to Sinsch (1988) common toads are leaving hibernation shelters in central Europe relating to actual climate conditions between March and April and they are migrating to breeding pond without feeding (Moore 1954, Heusser 1969). Breeding season is starting immediately after ice melting and toads are reaching water from beginning till end of April in south Sweden and Denmark with peak of activity in second half of this month (Gislén & Kauri 1959, Loman & Madson 1986, Höglund & Robertson 1987, Jörgensen et al. 1978). Migration starts in first half of March in mid Wales and culminating in the end of this month. Reproduction period is usually finishing there in the end of April (total duration=24–48 days) (Gittins et al. 1980). Reproduction period starts in the beginning of March and usually takes one month (09/03–11/04) in mid England (Davies & Halliday 1979). First toads reach water already 1st February and whole reproduction period takes till middle of March in south England (Cooke & Oldham 1995). According to Heusser (1968) and Sinsch (1987, 1988) reproduction period takes only one to two weeks in Germany. According to Leypold & Zavadil (1984) duration of reproduction period was 25 days and breeding finished around 10th May.

Together with many other toad's species (Licht 1976, Smith & Payne 1980, Fairchild 1981, Woodward 1982) also males of common toad are starting breeding season (Reading & Clarke 1983, Frazer 1966, Davies & Halliday 1979, Gittins et al. 1980a). Males are staying longer in water than females. Some of them spend there whole reproduction period. Females are leaving water already after a few days (Gittins et al. 1980a).

Day length and mean daily temperature trigger start of the spring breeding migration (Reading 1998) and temperature is a key factor affecting also course of breeding season of temperate anurans (Rühmenkorf 1958, van Gelder & Hoedemaekers 1971, Geisselman et al. 1971, Obert 1975, Beattie 1985, Bea et al. 1986). It is not easy to define any unambiguous threshold temperature separating activity from inactivity, because temperatures are usually fluctuating in the course of day/night and toads are responding to changes with some delete. Because most of toads are migrating during nights these temperature will be most important nevertheless their activity probably will affect also course of temperatures in previous a few hours.

Average air temperature 6.5 °C and minimal temperature 4 °C were climate conditions allowing toad's migration in south England. No toad migrated there in days/nights with temperature minimum 2.1 °C (Reading & Clark 1983). Temperatures 3.8 °C and 4.1 °C are limits for migration of males and females in mid Wales. Gittins et al. (1980a) observed toads leaving breeding pond during nights with air temperature dropping bellow this limit. According to Wisniewski et al. (1981) temperature limit for migration lies between 2 °C and 4.1 °C in mid Wales. According to Sinsch (1998) these results are reflecting limits of study methods rather than temperature limit of toads' activity and temperatures slightly above 0 °C allowing migration of common toads in Germany. Veith et al. (1979) considers 4 °C to be quite sufficient and 2 °C to be temperature limit in mid Germany. Air temperature was between 10–13 °C when first individuals of southern subspecies *B. b. spinosus* reached water (Sofianidou & Schneider 1985).

According to Reading & Clarke (1983) and Elmberg (1990) temperature limit is different according to latitude rather than to be constant for a species within its whole area of distribution.

Common toad *Bufo bufo* belongs among temperate amphibian species with biased sex ratio in breeding pond. Males over-number to females (Frazer 1966, Davies & Halliday 1977, 1978, Gittins et al. 1980a) during all reproduction season (Davies & Halliday 1979). This disproportion is general to all population regardless of locality (Reading et al. 1991).

Based on recapturing of previously marked animals sex ratio was 6.1, 3.6 and 10.2 (ø 5.4) in three successive years in Postupim and 9.1 and 9.4 in two successive years in Labe river area, Central Bohemia (Hodrová 1975). Sex ratio assessed by Obermajer (1985) in the same locality in Labe river area a few years later was as follows: 3.1, 3.3, 5.4 and 5.0. With reference to non-equal catchability of different animals in breeding population (Ricker 1969, Carothers 1979, Marten 1970, Bohlin & Sundström 1977, Buckland 1982, Hemelaar 1986) relating to common toad breeding strategy it is possible to consider data obtained by this method to be biased. Some authors mention that catchability of younger (Hemelaar 1986, van Gelder & Rijsdijk 1987) or smaller (Clarke 1972, van Gelder & Rijsdijk 1987) common toads is clearly lower comparing with elder or bigger animals. Non-equal catchability could be explained by different behaviour and breeding strategy of both sexes and different age and/or growth categories.

Based on catching of all breeding individuals total sex ratio in different localities was determined as follows: south Sweden first locality – 5.75 (Loman & Madson 1986), second locality – 2.54 and 1.72 in two successive years, third locality – 6.0 and between 1.9 and 8.2 in England relating to year and locality (Reading et al. 1991, Reading 2001) and 1.99 in Holland (Hemelaar 1986). Sex ratio from different west European localities mentioned by Hemelaar (1986) without detail localization was as follows: 5.66, 2.02, 2.06 and 1.92.

It case of interest regarding to competition among individuals in breeding pond it is useful to work with so-called operating sex ratio. This ratio is not stable in the course of breeding period and it reflects the best real situation in breeding aggregation of common toads. Average operating sex ratios of common toad from different localities were found as follows: 3.0 in Wales (Reading & Clark 1983), 6.0 in England (Davies & Halliday 1977), 4.5 in central England (Davies & Halliday 1979), 2.0 in England (Moore 1954). Despite the total sex ratio was 2.73 in England operation sex ratio fluctuated at the same locality between 2.5 and 12.7 in the course of one breeding season (Reading & Clark 1983). Disproportion was the highest especially during first half of breeding period.

According to Davies & Halliday (1977, 1978) in average 84.9% of all males is staying in breeding pond without females and contrary no any female was observed here without male. Gittins (1983b) and Wisniewski et al. (1980) mentioned similar data. Such a strongly biased sex ratio is caused by following reasons: females are spending shorter time in breeding pond and do not migrate here yearly (Davies & Halliday 1977, 1978, 1979, Gittins et al. 1980a), they are facing to higher mortality rate in sub-adult life period (Frazer 1966, Arak 1983b) and their sexual maturity is delayed (Smith 1951, Hemelaar 1985).

Operating sex ratio shifted in favour of males means also higher variability in reproduction success among males comparing with females. This phenomenon is sometimes enforced by multiple breeding success of some males at the account of other ones.

Opportunity for intra- and interspecies selection could be described as difference in reproductive success among individuals (Wade 1987, Wade & Arnold 1980). It is possible to distinguish two basic breeding strategies among temperate species of genus *Bufo* relating to duration of breeding period. Males of long-term breeders spend many weeks in breeding pond and attract females by vocalisation. For instance *Bufo calamita* is breeding from April till August in Germany (Bregulla 1986). Males are staying in water most of this time but females are arriving after a few days of vocalisation and staying here only short time till eggs laying (Mathias 1971, Flindt & Hemmer 1972, Arak 1983a). Females are choosing their partners according to vocalisation. Also males of some anuran species with short breeding period and with low breeding density are attracting females by voice (common spadefoot). Beside quality and quantity of male's vocalisation also time spending in water influences reproductive success of long-term breeders: *Bufo americanus* (Gatz 1981a), *B. woodhousei* (Woodward 1982, Sullivan 1987), *B. calamita* (Arak 1983b), *Hyla chrysoscelis* (Godwin & Roble 1983), *Hyla rosenbergi* (Kluge 1981), *Hyla cinerea* (Gerhardt et al. 1987), *Hyla crucifer* (Lykens & Forester 1987), *Centrolenella fleischmanni* (Greer & Wells 1980, Jacobson 1985) and *Rana virgatipes* (Given 1988). Intensity of vocalisation, frequency and duration are strongly influenced by air and water temperature (Forester 1973, Obert 1975, Brown & Brown 1977, Gerhardt & Mudry 1980, Fairchild 1981, Forester & Lykens 1986).

Common toad represents second reproduction system manifested by short breeding season, prevailing absence of vocalisation and intensive male-male combats. Strategy of vocalisation with limited movement would not be too effective in dense breeding aggregations. Males of explosive breeders are highly mobile in breeding pond. They are actively searching for females and they are ready to attack other males already in amplexus (Eibl-Eibesfeldt 1950, Davies & Halliday 1977, 1978). Males are not territorial (Wells 1977a, Davie & Halliday 1979, Elmberg 1986). Ability to get a female and to keep themselves in amplexus till eggs laying is crucial for them. Selection of breeding partners is nearly exclusively in hands of males.

Nevertheless above mentioned separation of long-term and explosive breeding anuran species is probably describing only two opposite ends of broad spectrum of reproduction strategies from one-night to whole year breeding season (Arak 1983a). Difference are existing among some subspecies and behaviour could divert relating to local conditions (Elmberg & Lundberg 1991). Partial differences in male breeding strategy were found also among not too remote (10–20 km or 60–100 m of high) populations of common toads (Kuhn 1994).

Males of giant toad *B.b.spinosus* are loudly vocalising and females are actively selecting their partners. They are either motionless during vocalisation or swimming in pond and not too seriously combating (Sofianidou & Schneider 1985). Also males of *B.b.bufo* subspecies are vocalising in breeding ponds with small population or low density. Nevertheless this behaviour is not common and their vocalisation is silent. It is possible to detect their voices in the end of breeding season when only a few males is present in pond (Heusser 1970).

Common toad is behaving like typical explosive breeders in England (Davies & Halliday 1977) and contrary like long-term breeders in Scandinavia (Höglund & Robertson 1988). Males of some anuran species are able actively adopt one of above-mentioned strategies (vocalisation or active female searching) according to actual density of competitors (Wells 1977b).

Whole-life male reproduction success depends on life span (Howard 1978), on reproduction season length (Wells 1977a, Arak 1983a) and on operational sex ration in breeding pond (Emlen & Oring 1977, Elmberg 1990).

The chance of males to get females is much bigger during main migration waves of females than during first days of migration. So why are males so hurrying to breeding pond? Is it possible to answer the question by different breeding strategies of small and big males?

84.4% of females was in amplexus already before water entering comparing to only 17.9% of males (Davies & Halliday 1979) resp. 79% of females and 20% of males (Vogrin & Miklič 2005). Reading & Clark (1983) mention 87.7–94.3% of females. On the contrary Höglund & Robertson (1987) claim that most of pairs is created in water. Such differences could be explained by deferent male strategies relating to climate conditions, size and density of population (Höglund & Robertson 1988, Savage 1961, Walkowiak & Brzoska 1982, Arak 1982, Tejedo 1988, Woodbright et al. 1990).

Solo males are usually staying in water after reaching of pond and they are patrolling close to shore or near banks during nights. However some authors (Savage 1934, Frazer 1966, Wisniewski et al. 1980, Gittins et al. 1980a) mention that some individuals leaving water and for a few hours are searching for females out of water. Loman & Madson (1986) detected that 2% of males patrolled as far as 100 meters out of water and Reading & Clarke (1983) mentioned 29% of such males.

Existing pairs are exposed to attacks of solo males from the moment of pairing till eggs laying. Bigger size of attackers is not necessary the rule (Höglund & Robertson 1987). Loman & Madson (1986) documented cases when smaller attacker displayed bigger males from amplexus nevertheless the opposite is far more common (Davies & Halliday 1978). Males from attacked pairs are kicking to attackers and are vocalising (Heusser 1970). Bigger males are advertising their body conditions by producing deep loud voice (Davies & Halliday 1978). However it is questionable why smaller males are vocalising as well.

Opportunity to assert better male body conditions in mutual combats is not probably equal in all common toad areas of distribution. Male's reproduction activity is concentrated mainly to nighttimes and length of nights is relating to latitude and period of spring as well. Nights are getting shorter northward and also with continuing springtime. So males from northern areas have less time for combats than males from southern areas (Elmberg 1990, Wells 1977a, Arak 1983a). Also delayed sex maturity of toads from north areas resulting in less biased sex ratio (Arak 1982) reduces advantage of male better body conditions.

50% of males were displaced from existing pairs (Gittins 1983), resp. 38% (Davies & Halliday 1978), resp. 11% (Loman & Madson 1986), resp. between 5% and 19% (mean=13.8), realting to year (Reading 2001). Some males (28%) paired already before water entering are loosing their females subsequently and approximately 1/3 of such winners is displaced from pairs again till moment of eggs laying (Reading & Clarke 1983). Davies & Halliday (1978) mentioned that both way of pairing (keeping of solo female or displacing of another male from existing pair) are useful strategies for breeding success of common toad males. 3/5 of eggs fertilising males got a solo females and 2/5 of such successful males displaced other males from existing pairs.

Combats finishing by multiple amplexus (more males attached to one female) could result in drowning of female. Females are avoiding to multiple amplexus by diving or swimming away (Davies & Halliday 1979). Especially habitats with shallow water and absence of detritus are potentially dangerous for females (Leypold & Zavadil 1984). These authors observed multiple amplexus also out of water.

Based on body dimensions there are two relations potentially influencing reproduction success (Loman & Madson 1986): 1) correlation of male and female body dimensions in pair and 2) influence of male body dimension to its ability to get a female.

(1) Male-female SVL correlation in pair: such correlation would reflect sexual selection based on body condition assessment of sexual partner. Some authors (Emlen 1976, Arak 1983b, Halliday 1983, Howard & Kluge 1985) suppose that such behaviour exists. Davies & Halliday (1977) confirmed this correlation in common toad pairs contrary to most of other authors (Gittins et al. 1980b, Hemelaar 1983, Reading & Clarke 1983, Smirina 1983, Loman & Madson 1986, Höglund & Robertson 1987). Hemelaar (1983) did not find any correlation between age of male and female in pairs before and during eggs laying as well. Density of toads in breeding pond could be a significant factor. Pairs with better balanced size dimensions have better chance to resist solo male attacks in condition of high male density (Arak 1983). According to Gittins et al. (1980b) approximately 7500 individuals of common toad creating breeding aggregation is sufficient for SVL correlation in pairs. In aggregations up 2000 individuals such correlation is not probable. According to Davies & Halliday (1977) and Ryan (1983) balanced SVL in pair positively affects eggs fertilisation nevertheless Höglund & Robertson (1987) mention that males are able to fertilize more than 90% of eggs regardless their SVL. SVL correlation could appear in different parts of breeding season. Relating to actual population density and intensity of males attacks weak SVL correlation could appear already in dry land (Gittins et al. 1980b). Small male is more easily replaced from big female than from smaller one in strong competitive pressure. Nevertheless Davies & Halliday (1977) found this correlation as late as in moment of eggs laying. Quick course of breeding season probably will not allow establishing of such correlation (Davies & Halliday 1977). These authors suppose that common toad female is able to influence selection of male fertilising her eggs. Contrary according to Gittins et al. (1980b) female can not influence partner replacement by walking or swimming through aggregation of solo males.

(2) Relation of male body dimension to breeding success: Such relation is supposing higher reproduction success of males with better body condition (Davies & Halliday 1977, 1979, Wilbur et al. 1978, Ryan 1980, Gittins et al. 1980b, Fairchild 1981, Reading & Clarke 1983). Nevertheless quick course of breeding season could reduce opportunity of bigger males to assert their advantage (Arak 1982, Höglund 1989). According to Boot (1982) and Davies & Halliday (1979) bigger males were not more successful in pairing before water entering nevertheless this relation was significant in moment of eggs laying. Gittins et al. (1980b) found this relation already before water entering. Also males leaving water and searching for females were significantly bigger. Multiple breeding success during one season is an exception among males (Savage 1961, Haapanen 1982, Höglund & Robertson 1987, Elmberg 1990) nevertheless it can occur and according to Loman & Madson (1986) such males belong among the biggest ones. Hemelaar (1986) and Höglund & Robertson (1987) did not find any SVL difference between males in amplexus and solo in any stage of breeding period.

Different frequency of sexual partners and competitors meetings expressed by density of males (Emlen & Oring 1977, Arak 1982, 1983, Olson et al. 1986, Tejedo 1988, Elmberg 1987, 1991) and/or different time disposing to males for combating (Arak 1982, Höglund 1989) could be an explanation of such contradicting results.

According to Gittins et al. (1980a) there is a tendency of bigger common toad males to delay their arrival because they are subsequently able to displace smaller males from existing pairs. At the other side Loman & Madson (1986) found tendency of bigger males to arrive sooner and stay in breeding pond for a longer time than smaller ones. According to them bigger males could await females in pond and than displace smaller ones from existing pairs. Small males could enlarge their breeding opportunity by pairing with females, usually arriving later on, in a dry land, where process of pairing is more random comparing with water combats. Sofianidou & Schneider (1985) found tendency of bigger individuals (*B. bufo spinosus*) of both sexes to arrive sooner.

METHODS

Breeding pond, located in Strnady, Central Bohemia (49° 56’ N, 14° 23’ E; 233 m a. s. l.), was enclosed by plastic fence in five succeeding spring periods 1991–1995 and toads were caught into pit-fall traps placed around fence. Toads were removed from traps every morning during all period of pond enclosure and continually in days with migration culminating. People living near of pond were informed about research not to disturb the ongoing project.

All animals were marked by toe-clipping and than released into pond. End of the same toe was cut off each year to all caught toads (marking was not individual). Subsequent casual control of animals in water was aimed to eliminate penetration of non-marked animals into pond. This method is time-consuming nevertheless analysis of toads’ activity is based on complete account of all individuals arriving to breeding pond. Toads trying to abandon enclosed area were released out of fence. Marking prevented their multiple involving into analysis. There was no any other suitable breeding place in broad surrounding area.

Ground air temperature was measured continually in pond vicinity and accuracy of data recording was adjusted weekly. Day (24 hours) averages, night averages (21:00–05:00) minimal temperature and maximal temperature were used for analyses. Water temperature was measured once a day near pond bottom always at the same place.

Following numbers of males and females were involved into analysis: 1991 – 670 males and 317 females, 1992 – 636 and 267, 1993 – 296 and 213, 1994 – 230 and 144, and 1995 – 149 and 106, respectively.

Beside total sex ratio and sex ratio in moment of start of mass eggs laying also fluctuation of operating sex ratio (operating sex ratio=sex ratio of toads presented in water during separate days of breeding season) was determined. Beginning of mass eggs laying means also end of the most male-male competition in breeding pond and sex ratio reflects potential chances of males to be reproductively successful in this moment. Ratio of common toads arriving to breeding pond already paired was determined separately for both sexes as well.

Random sample of males was used for analysis of correlation between date of arrival to breeding pond and SVL (snout-vent length) and weight respectively: 1991 – 62 (9.25% from total number), 1992 – 338 (53.14%), 1993 – 207 (69.93%), and 1994 – 224 (97.3%). These data were analysed by ANOVA followed by Scheffe’s test.

Table 1. Arrival of first individuals to the breeding pond

	1991	1992	1993	1994	1995
male	11/03	06/03	17/03	08/03	18/03
female	17/03	07/03	18/03	14/03	19/03

To test hypothesis about synchronisation of some male weight or SVL category with female migration, body conditions of males arriving during main female migration waves were compared with the rest of population. SVL measurement was done with accuracy of 1 mm and weight with accuracy 0.1 g. Only days with climate conditions allowing toad migration were taken into account. Also days with very limited numbers of arriving males were excluded because such data would negatively affected analysis.

Following numbers of toads were analysed for studying of male and female SVL relation in pairs: 128 pairs in 1992, 127 pairs in 1993 and 118 pairs in 1994. Relation was described by regression function and tested by coefficient of correlation for all three years separately and together as well.

SVL of 386 males arriving to water already in amplexus and 441 males arriving solo were compared to test influence of body dimensions to ability of males getting females already before water entering.

RESULTS

Migration of toads started always in March and except of 1991 year continued till April in the course of five breeding seasons 1991–1995. Figs 1–5 summarise breeding pond arrival date relating to temperature.

It is possible to postulate generally that toads' activity is responding to first longer period of warmer spring weather nevertheless migration is commonly interrupted by cool periods.

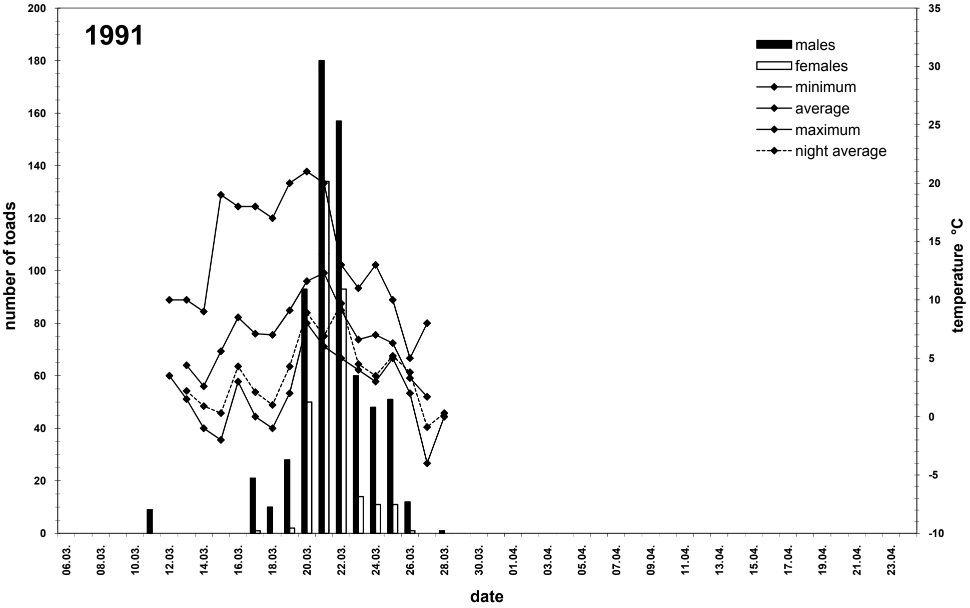

Fig. 1. Numbers of toads arriving to breeding pond and air temperature in 1991.

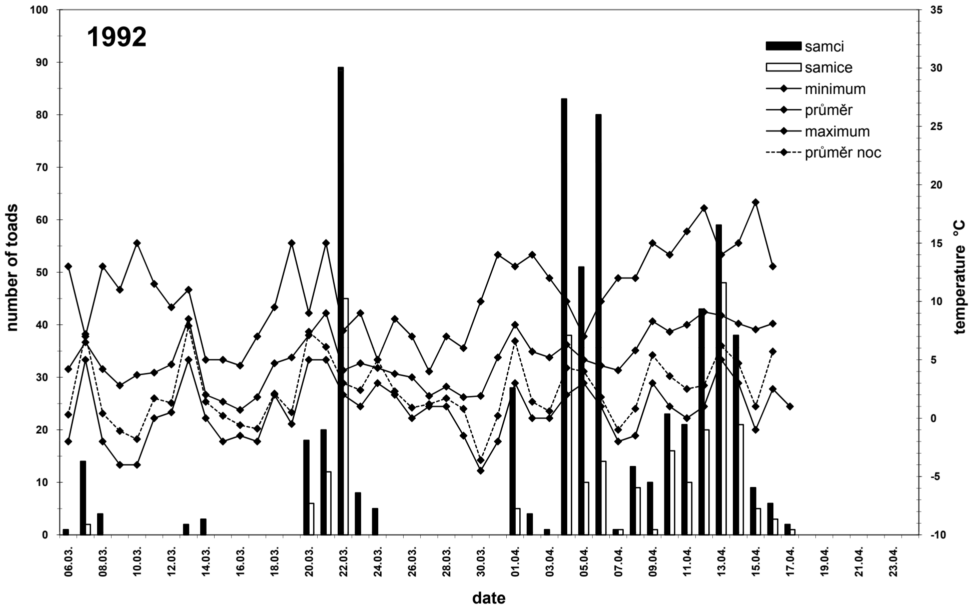

Fig. 2. Numbers of toads arriving to breeding pond and air temperature in 1992.

Migration peaks are caused not only as toads' response to temperature growing but also because individuals from greater perimeter are reaching breading pond.

Males are reaching breeding pond always before females (in average 3 days sooner).

The same tendency exists after cold periods interrupting migration. This mild difference is much stronger due to fact that males are far more numerous in beginning parts of migration. Till main (or first main) migration peak 7.9% of males reach pond comparing with 1.1% of females. Main or first main migration peak was detected 20/03/91, 20/03/92, 22/03/93, 24/03/94 and 02/04/95. Cold weather periods commonly interrupting migration are followed by another migration peak(s).

Duration of migration was 18 days (1991), 43 days (1992), 39 days (1993), 27 days (1994) and 34 days (1995) it means 32 days in average. Considering only days/nights with temperature allowing activity, toads were arriving during 12 days (1991), 27 days (1992), 19 days (1993), 17 days (1994) and 15 days (1995) it means 18 days in average.

Table 2. Sex ratio values (males/females) per particular year

year	total sex ratio	sex ratio at beginning of mass eggs laying	average operating sex ratio
1991	2.1	2.0	2.1
1992	2.4	2.8	2.8
1993	1.4	1.4	3.4
1994	1.6	1.8	2.1
1995	1.4	1.6	2.8

Table 3. Portion of toads paired before water entering

portion	1991	1992	1993	1994	1995
from total number of females	85.8	92.5	77.9	83.5	73.6
from total number of males	40.6	38.9	56.5	52.6	52.3
from paired males	85.8	92.5	77.9	83.5	73.6

During sharp temperature decrease the toads (both pairs and solo individuals as well) commonly left water. These individuals stayed in shallow holes near pond totally exposed to frost. Immediately after grow warmer toads arrived back to water. Nevertheless most of them reduced activity and weathered such periods at the bottom of pond.

Duration of total reproduction period from start of migration till mass water leaving was 22 days in 1991 (11/03–02/04), 46 days in 1992 (06/03–21/04), 42 days in 1993 (17/03–28/03), 30 days in 1994 (08/03–07/04) and 40 days in 1995 (18/03–27/04). It means 36 days in average.

Pair swimming in pond observed on 28/5/94 (41 days after end of breeding period) could be considered as an exception.

Temperature relating toads' activity in Strnady is summarized in figures 1–5. Toads were already migrating in nights with average temperature (21:00–05:00) above 2 °C nevertheless decrease of temperature during warmer period at this level means slowing down or even stopping of migration. Lower temperatures affect migration strongly at the beginning of migration period than during nights with culmination of migration. Average night temperature bellow 2 °C usually does not stop migration in such nigh, especially if precedes warm day. Males were exceptionally

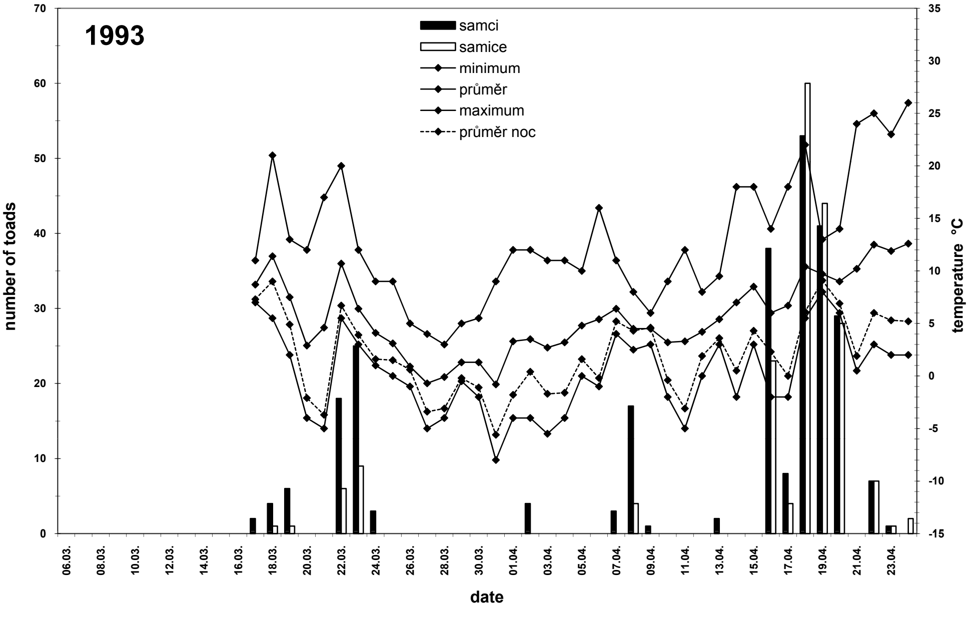

Fig. 3. Numbers of toads arriving to breeding pond and air temperature in 1993.

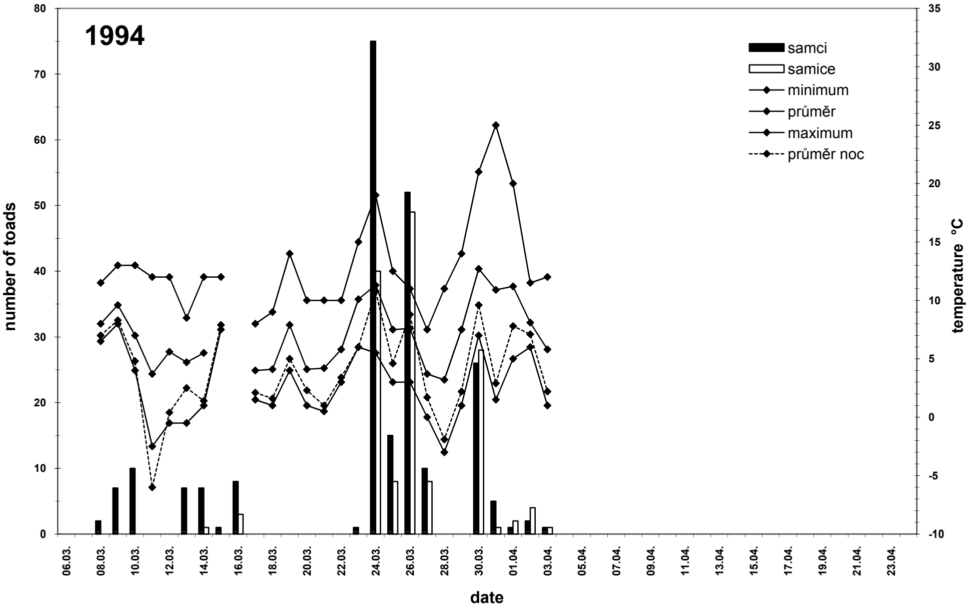

Fig. 4. Numbers of toads arriving to breeding pond and air temperature in 1994.

caught in pit-fall traps around pond also after nights with average night temperature 1 °C, 0 °C and even –1 °C. Nevertheless it does not mean that they are migrating in these conditions. It simply means that they reached water during warmer part of nights. Air temperature used to be higher in the beginning of nights and than is steeply decreasing till morning. Average night temperature bellow 2 °C is not sufficient for migration of males and females as well. Average night temperature 3.5 °C means that some males start to be active. 4 °C are quite sufficient for this sex while females are sometimes migrating but sometimes are not. Influence of preceding day temperatures likely play role. Migration of toads could be one day delayed after longer period of cold weather even if average night temperature equal to 5 °C. Migration is culminating when average night

Table 4. Results of analysis of variance (ANOVA) of snout-vent length of males arriving to the breeding pond in a course of particular years; * relation is significant

		degrees of freedom	mean square	f-criterion	p-value
1991	day	4	32.0861	1.7483	0.1520
	residuals	57	18.3530	–	–
1992	day	12	53.8776	2.6564	0.0021*
	residuals	326	20.2824	–	–
1993	day	12	28.1036	2.6468	0.0025*
	residuals	194	10.6181	–	–
1994	day	12	32.1505	1.8192	0.0467*
	residuals	211	17.6727	–	–

Table 5. Results of analysis of variance (ANOVA) of snout-vent length of males arriving to the breeding pond summarising four seasons (1991–1994)

	degrees of freedom	mean square	f-criterion	p-value
year	3	496.30254	28.3439	0
day	1	35.2147	2.0111	0.1565
year × day	3	156.9696	8.9646	0
residuals	823	17.51	–	–

temperature exceeds 6 °C. Minimal night temperature less than 0 °C signalises stopping of any toads' movement.

Rainfalls and ground moisture were sufficient during study periods and draught did not represent limit for migration.

Water temperature is not the same in different parts and depths of breeding pond and is fluctuating in the course of 24 hours even in such shallow and small water body. Toads are sometimes entering water with melting ice at the surface (years 1991, 1992, 1993) nevertheless water temperature near bottom was following: 5 °C in 1992, 4.5 °C in 1993, 6.5 °C in 1994, 5 °C in 1995. Water temperature was usually slowly growing in the course of breeding period with temporal fluctuation in range 4–8.5 °C (1991), 3–10 °C (1992), 4.5–14 °C (1993), 6–10 °C (1994), and 5–9 °C (1995), respectively.

Toads laid eggs in period 19/03–03/04 in 1990 (= 15 days) and 29/03–17/04 in 1992 (= 19 days). No any clear peaks in eggs laying activity were detected. Weather fluctuation was key

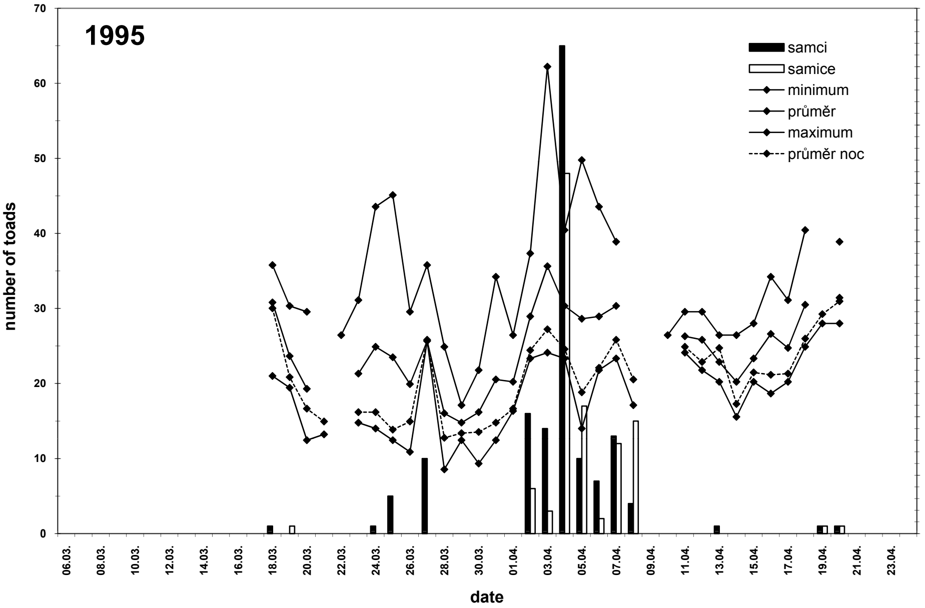

Fig. 5. Numbers of toads arriving to breeding pond and air temperature in 1995.

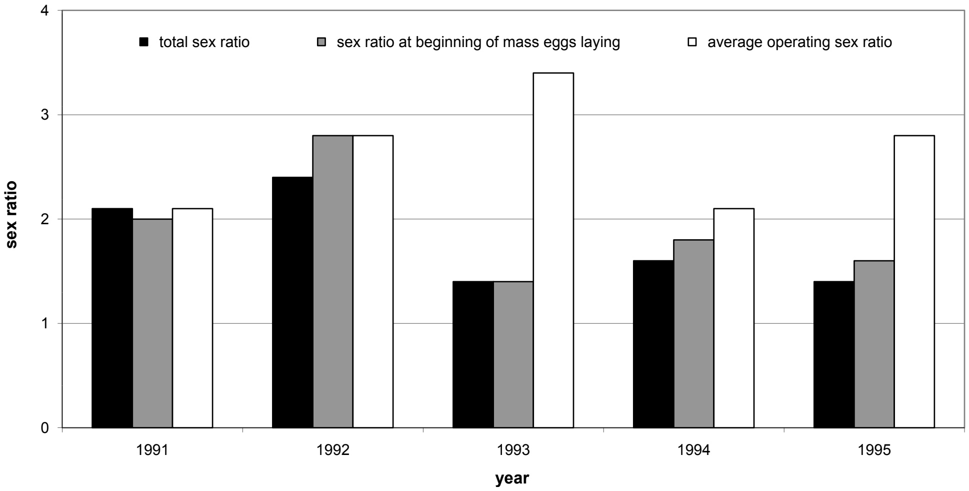

Fig. 6. Total sex ratio, average operating sex ratio and sex ratio in moment of mass eggs laying.

factor affecting toads' activity. First eggs were laid into water with temperature 7.5 °C (1991), 5 °C (1992), 6 °C (1993), 7.5 °C (1994), and 8 °C (1995), respectively.

Females are leaving water sooner after eggs laying but males are staying longer. Females leaving water after eggs laying with attached males were repeatedly observed in several seasons.

Figure 6 presents sex ratio values during five successive years (1991–1995) in breeding pond.

Figure 7 presents daily fluctuation of operating sex ratio in breeding pond during five successive years (1991–1995).

It is general that males are strongly over-numbering females during start phase of spring migration in breeding pond. This highly biased sex ratio is getting correct after night(s) when main, or first main, wave of migrating toads reaches pond. Females are already numerous among these migrants. Relating to year sex ratio was fluctuating between 3.1 and 1.4 from this moment in Strnady breeding pond.

Total sex ratio in breeding pond was fluctuating between 2.4 and 1.4 according to year (1991–1995).

Decrease of males in 1993 influenced statistical significant ($p<0.001$) shift of total sex ration between 1992 and 1993. Hypothesis about equality of total sex ratio values for all study years was tested and was rejected ($p<0.0001$). Reason of significant total sex ratio shift between 1992 and 1993 is not clear. Between-year changes were not significant neither before this shift (H_0:

Table 6. Comparison of males' SVL arriving during main females' migration wave and those arriving out of main migration wave (ANOVA) in 1992

	degrees of freedom	mean square	f-criterion	p-value
main wave	2	52.8714	2.4836	0.085
residuals	336	21.2882	–	–

Table 7. Results of ANOVA: relation between weight and date of males' arrival to the breeding pond in 1992; LOF = lack of fit (departure from linear trend in the relationship was tested)

	degrees of freedom	mean square	f-criterion	p-value
linear trend	1	454.48	8.6213	0.0037
LOF	11	82.2637	1.5605	0.1134
residuals	189	52.716	–	–

$P_{1991}=P_{1992}$, p=0.2509) nor after it (H_0: $P_{1993}=P_{1994}$, p-0.6230). Sex ratio stayed at lower level after this shift.

Start of massive eggs laying means end of most competition activities among males in breeding pond. Eggs laying pairs are not attacked any more. Relating to different seasons sex ratio in breeding pond was between 1.4 and 2.8 at this moment.

Portion of toads paired already before entering water is closely related to sex ratio of migrating toads. This portion is influenced in both sexes by actual number of arriving females, as a less numerous sex. Portion of females reaching water solo is increasing with growing of total number of females migrating at the same time but bigger portion of males is paired before water entering during these days/nights. It is reality that males have the biggest chance to get females already in dry land during main migration wave(s). And vice versa the most females enter breeding pond without paired males just during these days/nights. It seems to be advantageous for males (and especially for smaller ones) to concentrate their activity, either in water or around pond, just into such females' migration peaks.

Relating to females presence in breeding pond males had 5 days (1991), 23 days (1992), 30 days (1993), 6 days (1994), and 6 days (1995), respectively, for disposal to get a females, to compete each other or to keep themselves in amplexus till beginning of mass oviposition.

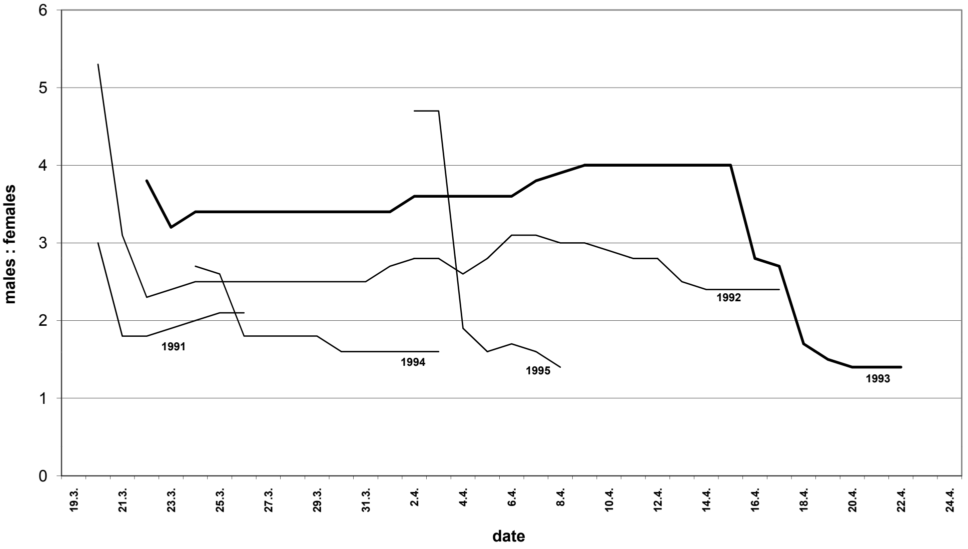

Fig. 7. Daily fluctuation of operating sex ratio in breeding pond during five successive seasons (1991–1995).

The ratio of females arriving already in amplexus was stable among years excluding year 1992. The same value was stale also for males nevertheless shift occured in 1993.

Relation between male SVL and time of water entering

Results of test dealing with relation between male snout-vent length and date of arrival to breeding pond are summarised in Table 4.

Relation between male SVL and date of arrival to breeding pond is not significant ($P > 0.05$) in 1991 year, nevertheless analysis showed significant ($P < 0.05$) negative relation in 1992 year (smaller males tend to arrive later than bigger ones). At the other side significant ($P < 0.05$) positive relation was found in 1993 and 1994 years (smaller males tend to arrive sooner than bigger ones). Following line equation are describing above mentioned relations:

1991: SVL=64.8607+0.2629 × number of days from the first water entering (1.3647) (0.1855);
1992: SVL=69.0379–0.0507 × number of days from the first water entering (0.6595) (0.0272);
1993: SVL=67.4112+0.0986 × number of days from the first water entering (0.7938) (0.0310);
1994: SVL=67.7187+0.1888 × number of days from the first water entering (0.7703) (0.0468).

Analysis of relation between male SVL and time of water entering summarising all four study years together shows absence of any consistent relation with general validity (see Table 5).

Following analysis was done to answer the question whether small or big males are timing their arrival to days/nights with the highest female migrating activity – main migration wave(s) – 22/3 and 4/4–6/4. SVL of males arriving during these days/nights was compared with rest of males in 1992 year.

68.880 mm (n=95) and 67.422 mm (n=147) are estimates of mean SLV of males arriving to breeding pond during first and second main migration waves. 67.872 mm (n=117) is estimate of mean SLV of males arriving out of these main migration waves.

SVL of males arriving during second main migration wave and those arriving out of any main migration waves was identical. Table 6 presents result of analysis of variance (ANOVA) of SVL of males arriving during first main migration wave and those arriving out of any main migration waves. Non-significant ($P>0.05$) difference means that neither small males nor big ones were synchronising their arrival to breeding pond with most intensive migration of females.

Relation between male weight and time of water entering

Relation between male's weight and date of arrival to breeding pond in 1992 year was tested by ANOVA. Significant positive relation between males weight and date of their arrival to breeding pond was determined. Following line equation is describing this growing trend: weight=34.9264+0.1585 **.** number of days from the first water entering (1.3277) (0.0548). This finding means that there is tendency of lighter males to arrive sooner than heavier ones.

SVL of males arriving to breeding pond solo versus SVL of males paired already before water entering

SVL of males arriving to breeding pond already paired was significantly ($P<0.01$) bigger (70.63±3.92 mm, n=386) than SVL of males arriving solo (67.83±5.56 mm, n=441).

Mate SVL assortment (male-female SVL correlation in pairs)

Significant positive correlation between SVL of males and females in pairs already before water entering was found. Following line equations are describing these relations for three seasons separately and all together as well: 1992: $Y=0.2195$; $X+73.734$; $r=0.1814$; $n=128$; $P<0.05$; 1993: $Y=0.1733$; $X+77.175$; $r=0.1233$; $n=127$; $P>0.05$; 1994: $Y=0.1103$; $X+85.562$; $r=0.0872$; $n=118$; $P>0.05$; 1992+1993+1994: $Y=0.2724$; $X+71.331$; $r=0.2010$; $n=373$; $P<0.01$.

DISCUSSION

Spring migration starts sooner in Strnady comparing with Sweden (Loman & Madson 1986, Höglund & Robertson 1987) or Denmark (Jörgensen et al. 1978), later comparing with south England (Reading & Clark 1983) and it is comparable with situation in mid Wales (Gittins et al. 1980a) or central England (Davies & Halliday 1979). Local climate conditions connected with altitude strongly define start and duration of toads' breeding activities regardless to locality.

The course and duration of migration and whole breeding period as well is influenced by temperature fluctuation. Differences are significant among years at the same locality. Comparing with data of Heusser (1968) and Sinsch (1987, 1988) from Germany and Cooke & Oldham (1995) from England reproduction period in Strnady was two to three times longer and similar with finding of Gittins et al. (1980a) from mid Wales resp. Reading (2001) from south England. Females' tendency to concentrate their activity into "migration waves" reflecting higher temperature and lower sensitivity of males starting migration and continuing also under worse climate conditions has general validity.

Toads leaving water during stronger temperature decrease observed in Strnady were mentioned also by Reading & Clark (1983), toads staying motionless near bottom by Davies & Halliday (1979).

Data about threshold temperature separating toads' activity from inactivity mentioned by different authors are not fully comparable because these results are strongly influenced by method of observation of toads and way of temperature measurement. Hypothetical limit or zone laid lower in Strnady comparing with data from south England (Reading & Clarke 1983, Frazer 1966 and mid Wales (Gittiens et al. 1980). Nevertheless it was comparable with findings of Wisniewsky et al. (1981) from another mid Wales locality (zone between 2 and 4.1 °C) and findings of Veith et al. (1979) from Germany (2 °C are considered to be minimal temperature allowing migration and 4 °C to be fully sufficient). On the contrary threshold temperature mentioned by Sinsch (1988) is laying lower (slightly above 0 °C). Such low temperature did not allow migration of toads in Strandy.

Most authors are in agreement that period of eggs laying takes one to two weeks, in Bavaria (Sinsch 1988), in England (Davies & Halliday 1978), in mid Sweden (Elmberg 1990). Most eggs have been laid from 18/04 till 24/04 in south Sweden (Loman & Madson 1986) and two peaks (02/03–11/03 and 14–24/03) were determined in England (Reading 1984). Toads are laying eggs in April in Bavaria (Sinsch 1988). These data are roughly in agreement with findings in Strnady.

According to Elmberg (1990), Haapanen (1982), Arak (1982) and Sjögren (1988) there is no any geographical trend among temperate explosive breeding anurans in duration of eggs laying period. Abundance of population and climate conditions are the most important factors. Females are more hurrying into eggs laying in localities with colder climate so higher level of synchronization among individuals (= shorter reproduction period) is visible there (Arak 1982, van Gelder & Hoedemaekers 1971, Sjögren 1988, Elmberg 1990).

Results relating to sex ratio from Strnady are in full compliance with data mentioned by other authors. Reasons of this biased sex ratio mentioned by other authors – shorter time of females' presence in breeding pond, more often skipping of some breeding season(s) and maturation in higher age, are valid in Strnady population as well.

The value of total sex ratio in breeding pond strongly differes among populations. Among years fluctuations of this value found in Strnady population are common although in another populations (Höglund & Robertson 1987).

Comparing with Hemelaar (1986), Loman & Madson (1986), Höglund & Robertson (1987), Reading et al. (1991) total sex ratio in Strnady belongs among less biased and values from years

1993 –1995 (1.4, 1.6, 1,4) are the lowest from all ever mentioned ones. Although average operating sex ratio in Strnady population is closer comparing with other European localities (Moore 1954, Davies & Halliday 1977, 1979, Reading & Clark 1983). Highly biased sex ratio in first half of migration period observed in Strnady is in accordance with finding of Reading & Clark (1983). This phenomenon is caused by delayed migration of females postponed to warmer spring periods.

Less biased sex ratio in Strnady is reducing level of male-male competition and is offering better chances for successful reproduction of more males.

Study method did not allow to confirm or to disconfirm multiple mating of some males.

Observed portion of females in amplesus already before water entering is corresponding to value 71% mentioned by Gittins et al. (1980b) and 79%, respectively (Vogrin & Miklič 2005). This portion is not significantly influenced by between-years changes in sex ratio in Strnady, nevertheless these changes are significantly ($P<0.005$) influencing this value for males.

Toads from Strnady are behaving like typical explosive breeders. Short breeding period is full of male-male competitions. Males are sometimes leaving water and patrolling at banks. It was possible to confirm findings of other authors that eggs laying pairs are no more attacked by other solo males nevertheless empty females leaving pond after finishing of eggs laying with males attached at their necks were observed.

Right timing of arrival to breeding pond could enlarge chances of males to get females. Small and big males could pose different strategy and timing their arrival differently. Such observations were done nevertheless results of different authors are contradictory (Gittins et al. 1980b, Gatz 1981, Loman & Madson 1986, Reading 2001). Analysis of male's SVL and date of arrival to Strnady breeding pond did not show any consistent among-year relation. Also neither small (= short) males nor big (= long) ones were timing their arrival into main females migration wave(s). Only one season was however analysed. Nevertheless SVL should not be the best criterion for separating different strategies of small and big males because there was, contrary to previous findings, significant correlation between body mass of males and their timing to water arrival (lighter males arrived sooner) in Strnady nevertheless only one season was analysed.

According to Boot (1982) chances of all males are equal in moment of water entering but chances of males in better body condition are going to grow with time spending in water between water reaching and starting of mass eggs laying. Short time means more random reproduction success (Arak 1982, Höglund 1989, Davies & Hallidaye 1979). Findings of other authors are only in partial agreement with above mentioned statement. Gittins at al. (1980b), Reading & Clark (1983) and Vogrin & Miklič (2005) mentioned better success of bigger males already before water entering and the same in moment of eggs laying. Hemelaar (1986) and Höglund & Robertson (1987) did not find any differences during all reproductive season. Selective advantages connected with better body conditions are likely quite often overlapped by external conditions (temperature, density of breeding population, parameters of breeding pond, etc) and their influence manifests only in some years. Over-wintering is likely main selective barrier for both sexes of common toad. According to Vogrin & Miklič (2005) also females in amplexus alredy before water reaching were much bigger than unpaire ones.

Bigger males were significantly more successful in pairing already before water entering than smaller ones in Strnady and subsequent testing of male's SVL vs. reproduction success was not undertaken.

Multiple reproduction success of some males (mating with more than one female during one season) mentioned by Reading & Clark (1983) was not detectable in Strnady by chosen study method nevertheless it is not too probable here regarding to short period of eggs laying.

Balanced rate of male and female SVL in pairs (size-assortative mating) seems to be advantageous for better eggs fertilization according to Davies & Hallidaye (1979) and Ryan (1983).

This statement is not however accepted by all authors (Höglund & Robertson 1987). While Davies & Hallidaye (1977) found significant correlation between male and female body lengths in amplexus before spawning other authors mentioned its absence (Gittins et al. 1980b, Hemelaar 1983, Reading & Clarke 1983, Smirina 1983, Loman & Madson 1986, Höglund & Robertson 1987). In spite of that SVL pairing assortment is the most probable in moment of eggs laying (Davies & Hallidaye 1979) such relation was observed in pairs already before water entering in Strnady population. This relation was highly significant. Size-assortative pairing already before water entering was confirmed also by Vogrin & Miklič (2005). Strong male-male competition already before water entering could be explanation. Small male is probably more easily removable from bigger female than from smaller one. Some authors also speculate about female ability to remove smaller males by displacing themselves to attacks of bigger males. Regarding to potential multiple amplexus, which is dangerous for females in water, such explanation does not seem to correspond with reality.

Another explanation was postulated by Reading (2001). Based on 20 years study he describes that pairing of common toads is not random with respect to the breeding experience of individuals. More inexperienced (first-time breeding) females were found paired with inexperienced (first-time breeding) males than could be expected. The mean proportions of experienced males and females arriving at the pond were highest during the first quarter of the breeding season. In contrast, the proportions of inexperienced males and inexperienced females arriving at the pond were lowest during the first quarter. Longer migration distances of first-breeders was an explanation.

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Middle Pleistocene birds from Petralona K-23, Greece

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Abstract. Middle Pleistocene deposits of Petralona K-23 yielded 203 identifiable fragments of avian bones. Most of them belong to small passerines, mainly larks (*Galerida* sp.). The avifauna indicates that open, dry ground was present in the vicinity of Petralona during the middle Pleistocene. The bones were probably assembled on the site by a small-bodied, ground-feeding raptor, such as *Falco tinnunculus*.

Aves, middle Pleistocene, Petralona, Greece

INTRODUCTION

Middle Pleistocene birds are known only from a few localities in continental Greece, including Petralona (Kretzoi 1977, Kretzoi & Poulianos 1981), Tourkobounia 5 (Mourer-Chauviré 1980), and Elaichoria 3 (Mlíkovský 1995).

In the present paper I describe a small collection of avian bones from a newly discovered site in the Petralona cave complex, Chalkidikidé, Greece. The geology and paleontology of the Petralona complex was described in detail by Poulianos (1996). Animal bones from the site K-23 originated in the earliest part of the middle Pleistocene, i.e. biozone Q 3_1 sensu Horáček (1981, Horáček & Ložek 1988) = MQ 2A sensu Mlíkovský (2002b).

Avian bones were collected in the site K-23 in 2000 by Ivan Horáček and Nikos Poulianos. They are deposited in the Museum of Petralona, Petralona, Greece (uncatalogized). Nomenclature and sequence of avian taxa follows Dickinson (2003). Minimum numbers of individuals were calculated according to Grayson (1984).

SYSTEMATIC LIST

Perdix perdix (Linnaeus, 1758)

Material. Distal end of left carpometacarpus, proximal end of left femur, distal end of right tibiotarsus, distal end of left tarsometatarsus, distal end of right tarsometatarsus; MNI=1.

Coturnix coturnix (Linnaeus, 1758)

Material. Proximal end of right humerus, distal end of right tibiotarsus; MNI=1.

Crex crex (Linnaeus, 1758)

Material. Proximal end of left humerus; MNI=1.

Table 1. Middle Pleistocene birds from Petralona K-23

taxon	bones	MNI	% MNI
Perdix perdix	5	1	5.3
Coturnix coturnix	2	1	5.3
Crex crex	1	1	5.3
Columba livia	3	1	5.3
Galerida sp.	40	14	73.7
Pica pica	1	1	5.3
Passeriformes indet.	151	–	–
Σ	203	19	100

Columba livia (Linnaeus, 1758)

MATERIAL. Proximal end of left scapula, sternal end of left coracoid, distal end of left humerus; MNI=1.

Galerida sp.

MATERIAL. 19 cranial ends of coracoids (10 left, 9 right), 21 proximal ends of humeri (7 left, 14 right); MNI=14.

REMARKS. Two south European species of this genus, *Galerida cristata* (Linnaeus, 1758) and *Galerida theklae* (Brehm, 1858) cannot be distinguished osteologically.

Pica pica (Linnaeus, 1758)

MATERIAL. Cranial end of left coracoid; MNI = 1.

Passeriformes indet.

MATERIAL. 4 proximal ends of scapulae, 12 cranial ends of coracoids, 7 sternal ends of coracoids, 8 proximal ends of humeri, 26 distal ends of humeri, 16 proximal ends of ulnae, 4 distal ends of ulnae, proximal end of radius, distal end of radius, 2 carpometacarpi, 19 proximal ends of carpometacarpi, 4 distal ends of carpometacarpi, 4 proximal ends of femora, 10 distal ends of tibiotarsi, 5 proximal ends of tarsometatarsi, 24 distal ends of tarsometatarsi; MNI=6.

REMARKS. All these bones belonged to small passerine species. Of the 12 cranial ends of coracoids, ten do not belong to the Alaudidae. Also the eight proximal ends of humeri do not belong to the Alaudidae. None of the bones listed here belongs to the Hirundinidae, Corvidae, and *Turdus* spp.

DISCUSSION

All identified bones belong to modern taxa, which are currently widely distributed in the western Palearctic (see Hagemeijer & Blair 1997).

Galerida, *Perdix* and *Crex* (87% MNI) are indicative of open, dry country. Also *Coturnix* (5% MNI) requires open country, but it is migratory and can thus be encountered in a wide array of habitats. *Pica* (5% MNI) prefers open country with some shrubs or trees. *Columba livia* (5% MNI) prefers open country with some cliffs for perching and breeding. All identified taxa of birds spend much of their life on the ground.

Bones of *Columba livia* could have originated from naturally died individuals, but bones of the remaining birds could hardly reach the cave unaided. They probably represent prey of a predator. Absence of large birds and predominance of birds weighting less than 50 g indicates that the predator was small-bodied. Absence of any tooth-marks and lesions on the broken ends of bones indicates that mammals were not responsible for the accumulation of avian bones at the site K-23. Main wing bones (humerus, ulna and carpometacarpus) of small passerines are much more frequent in the sample than main hind limb bones (femur, tibiotarsus and tarsometatarsus): 83:43 (all epiphyses counted). In the wing, all main bones are roughly equally represented (humerus : ulna : carpometacarpus = 34:20:27). This pattern is typical for raptors, excluding owls from further consideration. All identified taxa spend much time on the ground, which makes it probable, that the raptor caught its prey on the ground, which further excludes aerial feeding raptors. No extinct taxa of small-bodies raptors are known from Europe (Tyrberg 1998, Mlíkovský 2002a). A good candidate for the predator responsible for the accumulation of avian bones at the site K-23 is thus Common Kestrel *Falco tinnunculus* Linnaeus, 1758, recorded from other sites in Petralona (Kretzoi 1977, Kretzoi & Poulianos 1981). This species preys mainly on ground micromammals (which are much more frequent in the sample from K-23 than birds; I. Horáček, pers. communication), taking occasionally small ground birds. It often breeds in rock crevices. *Falco tinnunculus* was widespread in Europe from the early Pleistocene onwards (Tyrberg 1998, Mlíkovský 2002a).

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Isolated populations of *Zamenis longissimus* (Reptilia: Squamata) above the northern limit of the continuous range in Europe: origin and conservation status

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Abstract. This paper summarizes the current knowledge about isolated northerly populations of *Zamenis longissimus* (Laurenti, 1768) in Europe. Fossil records outside the present range are reviewed, suggesting a much wider distribution of the species during climatically more favourable periods of Holocene. Due to its geographical position outside of the continuous range, the origin of the isolated populations has long been debated. Despite a number of hypotheses proposed about their origin via human introduction, all evidence suggests that they are relics of the Holocene climatic optimum. Because isolated populations are particularly vulnerable to extinction but may harbour important adaptations to unfavourable conditions, all effort should be made to ensure their survival in the face of the current anthropogenic changes to the environment.

Isolated population, fossil record, origin hypothesis, management, Aesculapian snake, Europe, Palaearctic region

INTRODUCTION

Distribution of many European species has been influenced by Pleistocene climatic changes. The Aesculapian Snake, *Zamenis longissimus* (Laurenti, 1768) is not an exception. Recent isolated populations of the Aesculapian snake above the northern range limit, that are currently considered to be remnants of wider range at climatically more favourable periods, are known from Poland, Germany and Czech Republic (e.g., Böhme 1993, Mikátová & Zavadil 2001, Najbar 2000b, Schultz 1996). The northernmost one survives in the Ohře river valley in the Czech Republic beyond the 50° N. More than 200 km distance separates it from continuous range. This unique position of this population has evoked many hypothesis of its origin since the population was discovered in 1880 (Mikátová & Zavadil 2001). The Aesculapian Snake is undoubtedly most threatened and rarest snake of the Czech Republic as its continuous distribution extends only to the south and southeast of the country. Furthermore, factors as isolation from continuous range, very restricted area limited by microclimate, landscape changes and increasing anthropogenic pressure make the population in northwest Bohemia especially vulnerable (Haleš 1975, 1987, Mikátová & Zavadil 2001). Thus, evaluation of the status of this isolated population in the context of other European populations is a necessary prerequesite for the informed and efficient management.

DISTRIBUTION AND ECOLOGICAL REQUIRMENTS

Zamenis longissimus has a large distribution range extending from southern Spain to northwest Turkey including the following countries – south and central France, south and southwest Switzerland, northern Italy, Austria (thereof slightly expanding to include the Podyjí National Park in the Czech Republic), Slovakia (slightly extending to the Czech Republic in the White Carpathians Protected Landscape Area and Beskydy Protected Landscape Area), Hungary, Slovenia, Croatia, Serbia, Montenegro, Albania, Greece, Romania, Bulgaria, Moldavia and west Ukraine; disjunctive part of the distribution covers the eastern Black Sea coast to the Krasnodar region in Russia as well as parts of Georgia and Turkey (Böhme 1993, Günther & Waitzmann 1996, Schulz 1996).

The formerly recognised subspecies *Elaphe longissima persica* (Werner, 1913) from north Iran and southeast Azerbaijan and *Elaphe longissima romana* (Suckow, 1798) from Sicily and south and central Italy were recently upgraded to the species level [Lenk & Wüster 1999, Nilson & Andrén 1984, Utiger et al. 2002; nowadays *Zamenis persicus* (Werner, 1913) and *Zamenis lineatus* (Camerano, 1891)].

The Aesculapian snake is usually regarded as a thermophile species although this is not completely accurate. Humidity requirements are also important: it prefers moderately humid and warm places, and it avoids especially dry conditions (Gomille 2002). That is why it often occurs

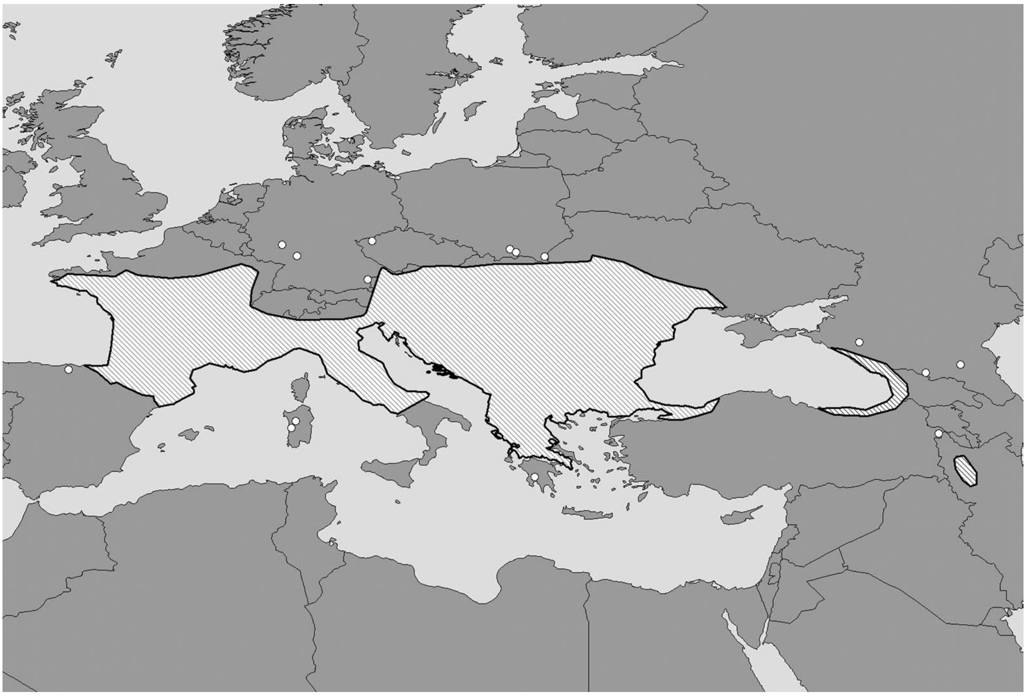

Fig. 1. Distribution of *Zamenis longissimus* (Laurenti) (according to Böhme 1993, Gomille 2002, and Schultz 1996); isolated populations are symbolized by white spots.

sympatrically with the Viviparous lizard, *Zootoca vivipara* (Jacquin, 1787). Nevertheless, higher temperature is necessary for successful egg incubation.

As described by Gomille (2002) the ecological requirements of the Aesculapian snake are reflected by the extent of its continuous range (Fig. 1). The southern, western and eastern limits of the distribution correlate with the range of summer-green deciduous forest that is dependent on precipitation. This type of forest is replaced by an evergreen Mediterranean forest at regions with low precipitation and high temperature, where the Aesculapian snake does not occur (predominant part of the Iberian peninsula, southern part of the Apennine peninsula and southeast Turkey). The northern range limit in central Europe appears to be determined by the temperature (Gomille 2002).

Occurrence at the northern edge of the range seems to be also determined by landscape morphology. Isolated populations are found in river valleys with woody slopes where microclimatic conditions might be of particular significance.

ISOLATED POPULATIONS AND THEIR HISTORY

There are a number of isolated populations of the Aesculapian snake off the limits of the continuous range. There is an isolated populatin near Urmia Lake in Iran, whose taxonomic status remains unclear (Nilson & Andrén 1984, Schultz 1996). Furthermore, isolated populations are known from east Georgia, Russia and Turkey near the eastern Black Sea Coast (Schultz 1996, Schweiger 1994 , Tunijev 1990).

Other isolated populations are located in southwest Spain and Sardinia below the southern range limit (Capocaccia 1965, Meijide 1973, Mellado et al. 1979) and in Germany, Switzerland, Denmark, Czech Republic and Poland above the northern range limit (e.g., Bayer 1894, Böhme 1993, Günther & Waitzmann 1996, Jaeschke 1971, Ljungar 1995, Mertens 1948, 1969, Mikátová & Zavadil 2001, Najbar 2000b, Reinhard 1938, Szyndlar 1984a, Šolcová-Danihelková 1966, Waitzmann 1993). These European populations (Fig. 2) are the focus of the present review.

Some of the isolated populations known from historical time have become extinct. The Danish population became extinct long ago. In the vicinity of Copenhagen, the species was still reported as common at the end of the 18th century (Boulenger 1913). Then three specimens were collected in the Danish island Zealand later in the 19th century, with the last one in 1863 (Hvass 1942). Because almost nothing was known about fossil records at that time they were viewed as introduced exemplars. Discovery of subfossil remains from Lystrup Enge area by Lujngar (1995) brought new light to this case, because now it could have been regarded also as relic of a once wider distribution range.

An isolated population near Basel in Switzerland became extinct quite recently. The last records date from 1971 (Böhme 1993).

Three isolated population are present in Germany today. They are located near Schlangenbad (Taunus Mts, Walluf stream valley, Hessen Province), near Hirschhorn (Odenwald Mts, Neckar valley, border of Hessen and Baden-Württemberg Provinces) and near Burghausen at the lower Salzach river (South Bavaria). The occurrence near Passau in the Danube valley, often described as an isolated population, actually belongs to the western branch of the continuous range extending to Germany from Austria (Waitzmann 1993). A population near Schlangenbad has been known since 1817 (Böhme 1993). Later, in 1905 an occurrence near Burghausen was recorded (Hecht 1928) and a third isolated area near Hirschorn has been discovered quite recently, in 1947–1948 (Mertens 1948).

According to Najbar (2000b, 2004b) there are six localities in Poland where the Aesculapian snake occurred in past and/or present. Złoty potok and Zamojszczyna populations are conside-

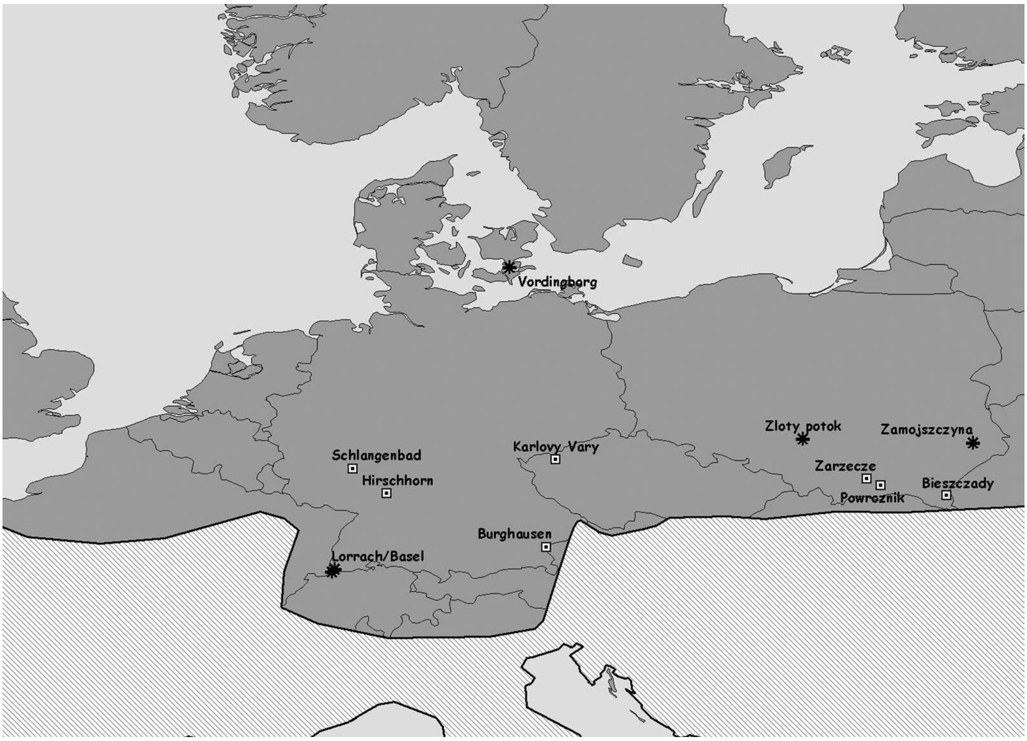

Fig. 2. Isolated populations of *Zamenis longissimus* (Laurenti) in Central Europe (according to Böhme 1993, Gomille 2002, and Schultz 1996), recent isolated populations are symbolized by squares, extinct ones by asterisks.

red to be the extinct, while at other localities (Zarzecze, Powroznik, Bieszczady Mts, Magurski National Park) Aesculapian snakes still occur.

The northern limit of the continuous range of *Zamenis longissimus* runs through southeastern Poland in the Bieszczady Mts, where only one known abundant population occurs. It may have been a peripheral population of the continuous range as described by Szyndlar (1984a), however it has lost contact with the continuous range and today is consider isolated (Najbar 2000a, 2004a). Additional records are recorded from Zarzecze (155 km from the Bieszczady Mts), Powroznik (115 km from Bieszczady Mts) and the Magurski NP (115 km from the Bieszczady Mts). But these are very scarce and of an unclear status.

The first written reference about the Czech isolated population in the Ohře river valley near Karlovy Vary in 1843 comes putatively from a Mr. Döbler, the librarian of the Count of Buquoy. This is reported by Šolcová-Danihelková (1966) as she obtained the information from Mr. Koudelka, the director of the Museum of Karlovy Vary. But this has never been confirmed. The first reliable evidence then comes from 1880 when Mr. Stýbal donated a specimen of the Aesculapian snake from Korunní (formerly Krondorf) to the National Museum in Prague (Bayer 1894, Štěpánek 1949, 1956, Vogel 1952, 1968, Záleský 1922). Vogel (1952, 1968) alleged that since that time nobody has noticed this species in Ohře river valley, however this is obviously not true. During the first half of the 20th century the Aesculapian snake was observed for example by Fieber (1932) and Reinhardt (1937, 1938). Two other specimens are deposited in the Museum of Karlovy Vary. One of them is surely dated before World War II and the second was caught in the mine of Stráž nad Ohří in 1956. Šolcová – Danihelková (1966) was the first to describe the population based on detailed field work. At that time the snake was spotted due to road reconstruction in very narrow part of the Ohře river valley between the villages Stráž nad Ohří and Boč. In the same year an exemplar of *Zamenis longissimus* was killed by a train near the village of Boč and deposited in the Museum of Plzeň (Tišer 1975). During next years the population is often mentioned by Haleš (1969, 1975, 1984 and 1987), Šolcová (1974), Janoušek (1979), Bárta (1983) or Šapovaliv & Zavadil (1990), nevertheless some of these authors intentionally do not specify localities for conservation reasons.

FOSSIL AND SUBFOSSIL RECORD

Fossil and subfossil records are known not only from the present distribution area (for example Italy, Austria, and Slovakia (e.g., Delfino & Bailon 2000, Ivanov 2007)) but also from many places outside the current range (Fig. 3, Table 1). Hence the Aesculapian snake must have occurred far more to the north and east than today in climatically favoured periods. Fossil remains from Pleistocene interglacials and also subfossil records from Holocene in the same localities in south

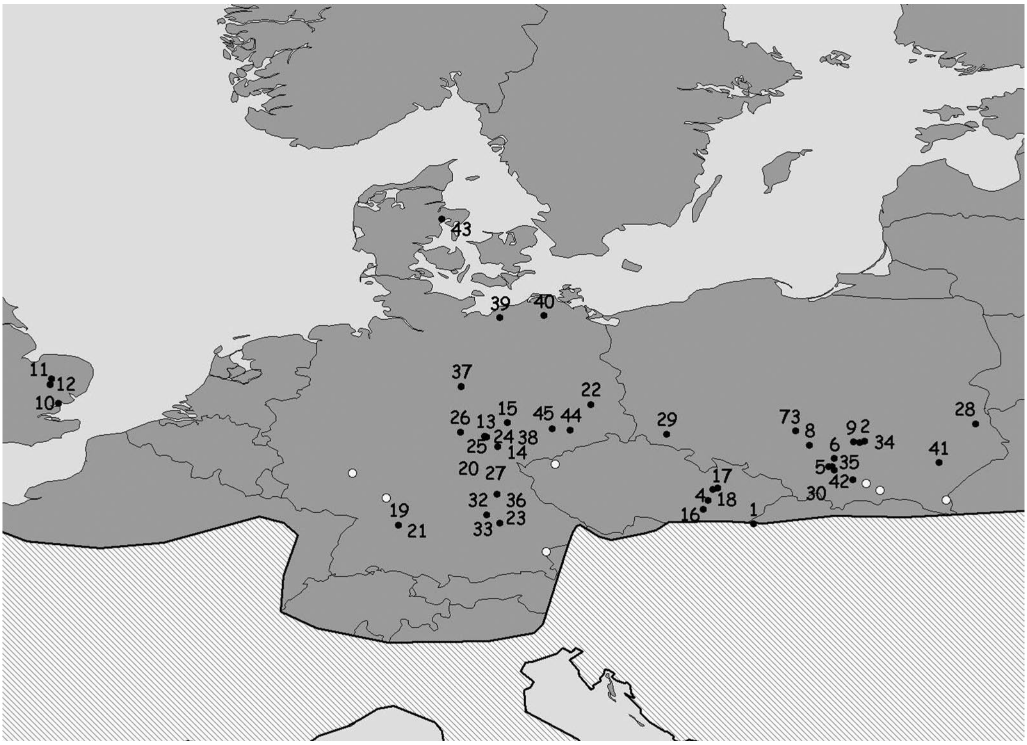

Fig. 3. Fossil record of *Zamenis longissimus* (Laurenti) outside its current range in Central and Northwest Europe (solid circles), numbers refer to Table 1, open circles represent isolated extant populations.

Table 1. Fossil records of the Aesculapian snake (*Zamenis longissimus* (Laurenti)) outside its current range from Central and North- western Europe; L = Lower, M = Middle, U = Upper

No.	locality	country	stage	reference
1	Ivanovce	Slovakia	L Pliocene	Ivanov (2007)
2	Kadzielnia	South Poland	L Pleistocene	Szyndlar (1984b)
3	Zalesiaki B	South Poland	L Pleistocene	Szyndlar (1984b)
4	Malá dohoda Quarry	Czech R., Moravian Karst	L Pleistocene	Ivanov (1996)
5	Kamyk	South Poland	L Pleistocene	Szyndlar (1984b)
6	Zabia Cave	Central Poland	L Pleistocene	Szyndlar (1984b), Ivanov (1997)
7	Zalesiaki A	South Poland	L to M Pleistocene	Szyndlar (1984b)
8	Zamkowa Dolna Cave	South Poland	L to M Pleistocene	Szyndlar (1984b)
9	Kozi Grzbiet	South Poland	L to M Pleistocene	Szyndlar (1984b)
10	Cudmore Grove	England, Essex, Mersea I.	M Pleistocene	Holman et al. (1990)
11	Barnham	England, Suffolk	M Pleistocene	Ashton et al. (1994)
12	Beeches Pit	England, Suffolk	M Pleistocene	Holman (1998 ex Gomille 2002)
13	Weimar-Ehringsdorf	Germany, Thuringia	M Pleistocene	Böhme & Heinrich (1994)
14	Gamsenberg	Germany, Thuringia	M Pleistocene	Böhme (2000)
15	Neumark-Nord	Germany, Saxony	M Pleistocene	Böhme (2001 ex Gomille 2002)
16	Stránská skála Hill	Czech R., Moravia	M Pleistocene	Ivanov (1995)
17	Mladeč Caves	Czech R., Morava	M Pleistocene	Ivanov (2006)
18	Za hájovnou Cave	Czech R., Moravia	M Pleistocene	Ivanov (2005)
19	Stuttgart-Bad Cannstatt	Germany, Baden-Württ.	M Pleistocene	Bottcher (1994)
20	Weimar-Ehringsdorf	Germany, Thuringia	M Pleistocene	Mlynarski & Ulrich (1975)
21	Stuttgart-Bad Cannstatt	Germany, Baden-Württ.	U Pleistocene	Bottcher (1994)
22	Schönfeld-Calau	Germany, Brandenburg	U Pleistocene	Böhme (1991b)
23	Lobsing	Germany, Bavaria	U Pleistocene	Heller (1960), Böhme (1997)
24	Weimar	Germany, Thuringia	U Pleistocene	Böhme G. (1989)
25	Taubach	Germany, Thuringia	U Pleistocene	Böhme G.(1989)
26	Burgtonna	Germany, Thuringia	U Pleistocene	Böhme G.(1989)
27	Gamsenberg	Germany, Thuringia	U Pleistocene	Böhme G. (2000)
28	Wierzbica	Central Poland	U Pleistocene	Szyndlar (1984b)
29	Rzasnik	East Poland	U Pleistocene	Szyndlar (1984b)
30	Zytnia Skala	South Poland	U Pleistocene/Holocene	Szyndlar (1984b)
31	Ciasna Cave	South Poland	U Pleistocene/Holocene	Szyndlar (1984b)
32	Malerfels	Germany, Bavaria	Holocene	Markert (1978 ex Gomille 2002)
33	Euerwanger Bühl	Germany, Bavaria	Holocene	Markert (1975)
34	Raj Cave	South Poland	Holocene	Szyndlar (1984b)
35	Niedostepna Cave	South Poland	Holocene	Szyndlar (1984b)
36	Grundfelsen Hohle	Germany, Bavaria	Holocene	Brunner (1942/3 ex Gomille 2002)
37	Kneitlingen	Germany, Lower Saxony	Holocene	Böhme (1991a)
38	Gamsenberg	Germany, Thuringia	Holocene	Böhme (2000)
39	Neukloster	Germany, Mecklenburg	Holocene	Peters (1977a,b)
40	Pisede	Germany, Mecklenburg	Holocene	Peters (1977a,b)
41	Jozéfow	South Poland	Holocene	Szyndlar (1984b)
42	Giebultow	South Poland	Holocene	Szyndlar (1984b)
43	Lystrup Enge	Denmark	Holocene	Ljungar (1995)
44	Robschütz	Germany, Saxony	Holocene	Böhme (1994)
45	Klosterbuch	Germany, Saxony	Holocene	Böhme (1991a)

Poland and Germany (Gamsenberg) indicate that the range of *Zamenis longissimus* repeatedly contracted and extended again during Quaternary (Szyndlar 1984b, Böhme 2000). Most important in the context of isolated populations are records from central and northwestern Europe (Fig. 3, Table 1).

Subfossil remnants of the Aesculapian snake from the Holocene period were found in northern Germany (Peters 1977a, b), southern Poland (Szyndlar 1984b) and Denmark (Ljungar 1995). The latter is the northernmost fossil record found until today and comes from the Lystrup Enge area. Dating was estimated to 4200–4000 years BC (Ljungar 1995). That corresponds with the Atlantic Period (7100–3750 years BC), climatic optimum of the Holocene, when annual mean temperatures were 2–2.5 °C higher than today (Dahl-Jensen et al. 1998). At that time for example the pond turtle, *Emys orbicularis* (Linnaeus, 1758) occurred even in Sweden close to 59°N (Sommer et al. 2007). Fossil remains have been discovered recently even in the Czech Republic. They come from the Lower or Middle Pleistocene periods and are located in Moravia (Ivanov 1995, 1996, 2005, 2006).

ORIGIN OF THE ISOLATED POPULATIONS

Isolated populations above the northern limit of the continuous range of *Zamenis longissimus* are today mostly regarded as a relic of a wider range in climatically more favourable conditions during the Holocene period (e.g., Gomille 2002, Ljungar 1995). Recent genetic analyses based on protein electrophoresis and mtDNA found no disagreement in the general phylogeografic pattern with this hypothesis for the German isolated populations (Joger et al. 2006, Joger et al. 2007, Lenk et al. 1995).

Nevertheless, their position far from the continuous range has provoked a long debate concerning their origin. The oldest known hypothesis comes from Heyden (1862 ex Böhme 1993), who considered the dispersal of this snake together with the Romans as cult symbol. Purportedly they introduced snakes around thermal spa they had founded. Because no other isolated population or fossil records were known at that time it quickly became a widely accepted explanation for the existence of the geographically isolated population near Schlangenbad (Gomille 2002). It was then cited by many authors, e.g., Brehm (1869) or Dürigen (1897) (both ex Gomille 2002), however soon it has appeared to be unsustainable due to a number of discrepancies. At first, the Aesculapian snake is found also around spas that were founded a hundred years after Roman expansion and also in areas that Romans have never reached (for example Karlovy Vary). Thus many other authors do not support this theory, such as Boulenger (1913), Reinhard (1938), Štěpánek (1949) etc. Moreover, further study has revealed that *Elaphe quatuorlineata* (Lacépède, 1798) rather than *Zamenis longissimus* might have been the cultic snake of Old Romans (Bodson 1981). However this Roman theory is still widespread among people as inferred from numerous web-based references.

Apart from the central Roman theory many local hypotheses attempt to explain the origin of the Bohemian isolated population near Karlovy Vary that are mainly spread by local people. The first theory about introduction by the Count of Buquoy was already mentioned above. This should have been recorded in chronicle by Mr. Döbler but has never been confirmed (Mikátová & Zavadil 2001). The theory has been fist mentioned by Šolcová-Danihelková (1966). Another hypothesis accepted by local people is introduction by the Mathoni family around 1880. However, there is no evidence to support even that assumption. Introduction by Avramides, a Greek merchant who worked in mineral water company in Korunní Kyselka is the last hypothesis. If this were true, the introduction should have happened in first half of the 20th century. The theory is inconsistent with regard to the fact that the first specimen was already captured in 1880. Furthermore, John Bey Avramides several times called specialists attention to the rare occurrence of this snake (e.g., Reinhardt 1938) and hence it is very unlikely that he would have forgotten to mention that he introduced them himself.

The fact that people really tried to introduce Aesculapian snake in many places in Europe might have contributed to formation of various origin hypothesis even of natural populations. The oldest known case of intentional introduction happened close to Schlitz in 1853/1854. Here the Count of Görtzu released circa 40 animals. This population reproduced for the next tens of years but eventually became extinct (Böhme 1993). Jaeschke (1971) was the last one who observed this species at this locality. In the area of the present Czech Republic there were several attempts during the 1980s to introduce the species at localities where it did not occur naturally: for example near Vráž u Berouna and around Slapy Dam (Mikátová & Zavadil 2001), which were unsuccessful in both cases. However, there is an introduced population in north Wales in Great Britain (Edgar & Bird 2005) and in 1994 there was a first announcement about an illegal introduction in Switzerland in a vineyard near the Lac de Bienne (Hofer 2001).

CURRENT STATUS AND FUTURE PROSPECTS

According to Böhme (1991a), herpetofauna of Central Europe is nowadays in withdrawal phase after their maximal expansion in Holocene climatic optimum, so isolated populations are naturally threatened by range contraction caused by climatic deterioration since the Atlantic period of Holocene. The range of the Aesculapian snake has been slowly contracting since this period. However, this natural and gradual process can be made significantly faster with anthropogenic pressure. Habitat alteration and destruction, intensive agriculture or forestry, land consolidation, urbanization, and quarry recultivations are among the most serious threats (Waitzmann 1993). On the other hand, the opposite processes as leaving agricultural land without care and succession leads also to a habitat that is unfavourable for snakes. These factors may have been the reason for the extinction of the Danish population that went extinct in the 19th century, although natural habitat and climatic changes could have also been important. However, an isolated population on the Swiss-German border near Basel and a population near Zloty Potok and Zamojszczyzna in Poland became extinct only a few decades ago. At the latter locality the Aesculapian snake was still described as a frequently met snake in 1910–1912 (Najbar 2000b). The situation of the Polish isolated population is undoubtedly the most critical among recent isolated populations with no chance for recovery. According to Najbar (2000b, 2004a) the territory habited by *Zamenis longissimus* decreased rapidly during the last few decades. Moreover, the territory split to three separate areas that do not appear to communicate with each other. The core area inhabited by Aesculapian snake used to be up to 57 km^2 in post-war term, then 8.5 km^2 later in 1990–1995 and in the years 1999–2003 the area shranked only to 4.0–4.5 km^2 (Najbar 2000b, Najbar 2004a). The same trend can be seen in the numbers of specimens observed in different periods. The first estimations made in the 1990s talked about more than 200 animals, today it is roughly 75 specimens divided into three separated areas Najbar (2000b, 2004a). Even very strict conservation measures that came into effect in 1995 probably will not reverse the decreasing trend.

On the other hand, German isolated populations have been studied intensively since the 1980s. The population near Schlangenbad was studied by Heimes (1988, 1989, 1991), near Hirschhorn by Waitzmann (1989) and Gomille (2002) and the last one near Burghausen is less explored in comparison to them however sufficient study has been completed (Assmann & Drobny 1990). These authors did not feel confident to establish population size estimates and dynamics of German isolated populations due to lack of prior data for comparison. But the abundance can be deduced from the number of captured animals. The number is 190 specimens during seasons 1988 and 1989 (Waitzmann 1989) and 113 animals in 1998 (Gomille 2002) near Hirschhorn and 215 exemplars in 1988 (Heimes 1989) near Schlangenbad. These early studies certainly contribute to management and today's positive status.

The Bohemian population in the Ohře valley has been under some type of study since the 1970s (Haleš 1975, 1984, 1987, Janoušek 1979, Šapovaliv & Zavadil 1990, Zavadil & Šapovaliv 1990). According to Haleš (1987), a rapid decline in abundance has been documented since the 1980s, mainly due to habitat alteration and destruction. Another point worth mentioning is the unusually high degree of synantropism (Haleš 1987). The same was observed in Germany as snakes live alongside people: inhabiting their gardens, outhouses, barns and even garrets (Waitzmann 1993). This synantropism might be consequence of unusually high population density, harsh climatic conditions and progressive succession. Managed dwelling areas can provide enough food and cover and also manmade egg-laying sites that are highly important in these climatically less favourable conditions.

In conclusion, the isolated populations of *Zamenis longissimus* are highly vulnerable to extinction because of their position above the northern range limit. Considering the fate of most other isolated populations in Europe it is evident that the isolated population in the Czech Republic may be close to following the same trend as those in, e.g., Poland. Once the isolated populations become extinct, there is no possibility of immediate natural restoration due to the spatial remoteness and habitat separation from the nearest extant populations. However, the loss of isolated populations may have important consequencies for the entire species. For example, isolated northerly populations may show various types of ecological and physiological adaptations to less favourable climatic and environmental conditions that could be important for the response of the species to changing climate but that would be lost with the extinctions of these populations. Therefore, all effort should be made to preserve these populations and to understand their ecological requirements and evolutionary adaptations to the environment they occupy.

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Václav Skuhravý: 80th Birthday

Václav Skuhravý celebrated his 80th birthday in April 2008, which makes this a good time to review the major contributions that he, and his wife Marcela Skuhravá, have made to the study of gall midges, and of other insects, in Europe over the past fifty years.

Václav was born at Kadov, South Bohemia, on April 1, 1928 and attended the local grammar school at Příbram from 1939 to 1947. He then enrolled in the Faculty of Biology, Charles University, Prague, graduating in 1951 and joining the staff as a senior lecturer. It was here that he met Marcela, who was a student in the Faculty, and so began a remarkable collaboration in the study of European gall midges. They married in 1955 and have a daughter, Ivana, and a son, Pavel, plus six grandchildren.

In 1954 the Czechoslovak Academy of Sciences established an Entomological Laboratory, which later became the Czech Institute of Entomology. In 1962 Václav was one of the founding members of the Institute, working as head of the Department of Insect Ecology from 1962 to 1970, at first in Prague and then, from 1985 he worked in České Budějovice. Throughout this career his main interests have been in insect ecology, with particular emphasis on pest species, and he pioneered many improvements in long-term field studies of pest populations and the use of non--chemical controls to reduce environmental damage. In addition to his studies on Cecidomyiidae, he has made important contributions to research on the biology, ecology and control of insect pests in agriculture (Colorado beetle, *Leptinotarsa decemlineata;* beet leaf miner, *Pegomyia betae* [now *Pegomya hyoscyami*]) and in forestry (spruce bark beetle, *Ips typographus*; larch tortrix moth, *Zeiraphera diniana* and black arches moth, *Lymantria monacha*). Biographies, including bibliographies of Václav's scientific work, were published on the occasions of his sixtieth and seventieth birthdays (Novák, 1990; Rusek, 1999) and an updated selected bibliography is appended here. It is hoped that a full bibliography of both Václav's an Marcela's publications will soon be available on a website that they are preparing. This will record sole or joint authorship of about 260 scientific papers and of 14 books, including *Zoological Prakticum* (1954), *Die Rübenfliege* (1967), *Breeding Methods of Insects* (1968), *South Bohemia, Environment and its Protection* (1982), *The larch bud moth, Zeiraphera diniana* (1985), *The needle-shortening gall midge*, *Thecodiplosis brachyntera* (*Schwägr.*) *on the genus Pinus* (1991) and *Spruce bark beetle* (*Ips typographicus*) *and its outbreaks* (2002).

His interest in gall midges (Diptera: Cecidomyidae) developed in this context and has now persisted for more than fifty years. Marcela first published on gall midges in 1957 and in 1960 they co-authored a booklet on gall midges in Czechoslovakia. Later, in 1963, with a second edition in 1973, they published another booklet entitled *Gallmücken und ihre Gallen auf Wildpflanzen,* which is an excellent account, illustrated with black and white photographs and line drawings of galls. Since then they have produced more than 100 publications on the occurrence, distribution, biology, ecology, taxonomy and economic importance of gall midges and have more in press. This is a major and remarkable joint contribution to our knowledge of the Cecidomyiidae and seems unlikely to be surpassed in these days of short-term research projects. Throughout this period of half a century their enthusiasm and drive has been maintained and they are as productive now as they were at the beginning.

During the Soviet era communication and travel were difficult and their field work was restricted to Eastern Bloc countries. This work began in the 1950s and first resulted in thorough field surveys of the gall midges of Czechoslovakia [now the Czech Republic and Slovakia], during which they developed standardised techniques for recording the distribution of species, based on visual searching for galls at selected locations. Political changes in the late 1980s gave them freedom to travel and to collaborate more widely and up to August 2008 they have been involved in reviews and surveys of gall midges in Austria, Bosnia, Bulgaria, Croatia, Cyprus, Denmark, France, Germany, Greece, Italy, Hungary, Lichtenstein, Macedonia, Malta, Mallorca, Montenegro, Norway, Poland, Romania, Russia, Serbia, Siberia, Slovenia, Switzerland, Turkey, Yugoslavia, and the UK. Their total up to the end of 2007 was 1,824 localities visited throughout Europe and marginally into Asia (in Turkey and Central Siberia), which must be an all-time record and gives them considerable insight into the biogeography of gall midges. In some cases their personal observations have greatly increased the number of known species within a country, as for example in Greece, where they added 169 species to the previous total of 18 and in Austria where they have added 151 species to the pre-1967 total of 245 species.

But this is only part of their contribution as they have also been involved in taxonomic work at various levels, including Marcela's authorship of the Cecidomyiidae section in the *Catalogue of Palaearctic Diptera* (1986) and of the relevant section of *Contributions to a Manual of Palaearctic Diptera* (1997).

Although now well beyond retirement age, they are still busy with many projects. Among these, the spread across Europe of the horsechestnut leaf miner, *Cameraria ohridella* and of the North American gall midge, *Obolodiplosis robiniae* have been of particular interest and Václav is currently writing a book on the history of entomology in the Czech Republic, which will be his personal account of the development of entomological research during the military and political changes that have affected the country during his lifetime.

Marcela Skuhravá and Václav Skuhravý in the UK (September 2006)

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